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ERRATA

Page 346, lines 6 and 7 and lines 41 and 42: for "Dr. E. Berkeley" read "Mr. and Mrs. C. Berkeley."

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CHANGES IN THE OSMOTIC VALUE OF THE EXPRESSED SAP OF LEAVES AND SMALL TWIGS OF *LARREA TRIDENTATA*[1] AS INFLUENCED BY ENVIRONMENTAL CONDITIONS

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[1] *Larrea tridentata* Cav. = *Covillea tridentata* (DC.) Vail.

[2] The writer gratefully acknowledges the helpful suggestions, kindly criticisms and other aid given him during the course of this investigation by Dr. Forrest Shreve, in charge of the Desert Laboratory; Dr. B. M. Duggar, University of Wisconsin; Dr. Heinrich Walter, University of Heidelberg; and Mr. R. A. Greene and Mr. H. V. Smith, University of Arizona.

Contents

CHANGES IN THE OSMOTIC VALUE OF THE EXPRESSED SAP OF LEAVES AND SMALL TWIGS OF *LARREA TRIDENTATA* AS INFLUENCED BY ENVIRONMENTAL CONDITIONS

Introduction

A great amount of experimental research has been done on the effect of environment upon the concentration of the cell sap of plants. The most noteworthy and extensive contributions to this phase of botanical research are those of the late J. Arthur Harris and his colleagues (1915-1921) who have emphasized the value of such work in ecological and phytogeographical studies.

One of the chief influences of the environment upon the cellular activity of a plant is manifested in changes in the moisture content of the plant tissues and many determinations of the moisture content of plants and of plant parts have been made for the purpose of obtaining a measure of this influence. However, such measurements indicate only the total moisture content of the tissues and do not give the distribution of that moisture. Measurements of the osmotic pressure of the cell sap, on the other hand, while they do not show the amount of water present, indicate the condition of the water, which is of far greater significance for the plant and much more indicative of the plant's welfare. All metabolic activities of a plant take place in solution and their rate is largely determined by the degree of saturation of the plant tissues. Determinations of the changes which occur in the concentration of the cell sap of a plant from time to time therefore furnish a very good indication of the influences of the environmental conditions upon the plant.

The term "osmotic value" is a better one to use when referring to the concentration of the cell sap, since the osmotic pressures obtained for plant tissues are always subject to the accuracy of the method used in determining them. Ursprung and Blum (1916) are credited with having originated the symbol "Ov" to designate this value.

Numerous investigations dealing with winter hardiness and with drought resistance have shown that each species of plant is limited in its response to environmental conditions by a definite range of osmotic values for its cell sap, and this range is specific for a given species. Recently, Walter (1929) has emphasized the fact that not only may each species of plant experience a range in osmotic values throughout which it can survive successfully, but that each species is characterized by a somewhat definite rate of change in the osmotic value of its sap as conditions for development become more favorable or less favorable to the individual plants. During the severe cold period which occurred from January to March 1929 in Europe, *Hedera helix,* with a range of osmotic values from 14 to 24 atmospheres, was killed while *Pinus silvestris,* which has the same osmotic inertia, was not killed. The latter

possesses a higher maximum value and the cold period broke before that maximum was reached. *Buxus sempervirens*, on the other hand, with a range of osmotic value from 33 to 72 atmospheres has less osmotic inertia than the other two species and the maximum osmotic value was just reached at the end of the period of extremely low temperatures and therefore only a small amount of killing of this plant occurred.

The purpose of the work herein reported is to determine the range and differences in the rate of change of osmotic values prevailing in *Larrea tridentata* under natural conditions of growth over a considerable period of time and to attempt to correlate these variations in range and rate of change with factors of the environment.

Larrea tridentata is commonly called "creosote bush" because of the creosote-like odor which is produced when the plants become wet. Erroneously the creosote bush is sometimes called greasewood.

Under usual conditions *Larrea tridentata*, which is placed in the Zygophyllaceae, appears as a dark brownish green shrub from 4 to 6 feet high. It is an open type of bush; the main branching occurs in the crown at the surface of the ground. The dark brownish green color is due partly to the thick resin-covered leaves and partly to the fact that during a greater part of the year a certain quantity of dead leaves are present on the bushes. The leaves are quite small and are most abundant on the young twigs.

Several reasons might be advanced for selecting Larrea for this investigation. One is its wide distribution in the southwest. Shantz and Piemeisel (1924) state that in the southwestern desert region the creosote bush association is the most important type of vegetation. Its range of distribution extends from the Mohave desert nearly to central Texas and in southwestern United States and northwestern Mexico. Larrea is found at all elevations from sea level to 4,000 feet.

The creosote bush, which is a non-succulent, slow growing, shrubby perennial, is very drought resistant, as might well be expected of a plant with such a distribution range. Harris and Lawrence (1916) made the observation that the occurrence of Larrea as the dominant plant over thousands of square miles of territory in the arid southwest is proof that it is one of the most successful of the desert perennials. The drought resistant qualities of this plant arouse even more profound respect when we realize that it inhabits the most xeric areas, excepting the salt spots, which the southwestern desert embraces; namely, the bajadas or outwash slopes.

Livingston, in the publication of Spalding (1909), while writing on the dryness of the bajadas, observes that this condition probably accounts for the absence here of almost all vegetation excepting the characteristic Larrea and a number of forms which are active only during the rainy seasons. In connection with his work on the root habits of desert plants, Cannon (1911) found that for the period of his studies the soil of the bajada did not contain

sufficient water for shallow-rooted plants for more than three weeks of the year. It appears therefore that the bajadas are very xeric habitats and that the creosote bush is the chief plant inhabitant of these areas.

Another reason for the selection of *Larrea tridentata* for these studies is the fact that it makes successful and persistent growth in relatively thin bodies of soil over layers of hardpan. In Arizona the hardpan, or caliche, as it has been called since the days of the early Spanish settlers, is always calcareous in nature and, as pointed out by Breazeale and Smith (1930) is formed by the solution, transportation, and precipitation of calcium carbonate.

The soil solution of areas underlaid with caliche contained at one time considerable quantities of calcium bicarbonate, and probably still do. It was included, therefore, as a part of these investigations, to determine whether there is any marked relationship between the mineral content of the soils in different creosote bush areas and the variations in the osmotic values of the cell sap of the plants.

MATERIALS AND METHODS

Four areas were selected within a radius of twenty miles of the Desert Laboratory in which the dominant species in the plant association is the creosote bush. These areas were representative of the habitats, both good and poor, in which Larrea grows in the vicinity of Tucson.

At a representative location within each area a plot of approximately 100 square feet was staked out and all samples from each of the areas were taken from plants or soil within the limits of the respective squares. In fact, all of the leaf samples and weekly soil samples from any given plot were taken within a radius of thirty feet or less.

A description is given below of each of the four areas studied including a designation for each location which is intended to aid the reader in keeping in mind some of the features of the areas under discussion.

Area CB was so designated because it is located on the southern outwash slope or bajada of the Santa Catalina mountains three miles directly south from the entrance to Pima Canyon and about one and one-half miles north of the Rillito River. The creosote stand on this area is not as pure as those on the other three areas, being interspersed somewhat with *Carnegiea gigantea, Parkinsonia microphylla, Franseria deltoidea, Encelia farinosa,* a few small perennials and, in season, a few winter and summer annuals. However, within the particular plot chosen for study on this area neither of the large perennials Carnegiea nor Parkinsonia occurs and Larrea is by far the largest and the dominant plant. The soil is of granitic origin and "caliche" occurs at a depth of 12 to 24 inches below the surface. The creosote bushes here are 4 to 8 feet in height.

Area CP was selected primarily because the caliche or hardpan layer comes very close to the surface and is covered by only 6 to 12 inches of soil. In many places in the immediate vicinity large sheets of caliche are visible

at the surface. The caliche prominence lead to the selection of the designating letters "CP." This habitat is about 10 miles to the south and slightly east from area CB. Associated with Larrea, which is the dominant plant on this area, is a small herbaceous perennial *Crassina pumila* and a few winter and summer annuals which are active only during the rainy seasons. The bushes on this area have the poorest appearance and show the least amount of growth of those on any of the selected plots. They attain a height of only 3 to 4 feet; the older leaves are for the most part comparatively smaller; and a larger percentage of dead branches is present.

Area TB was so designated because of its geographical location on the westerly outwash slope or bajada of the Tucson mountains, 15 miles west of the Desert Laboratory. For all practical purposes this area represents a pure stand of Larrea at all seasons of the year. Only a few scattered representatives of *Echinocereus wislizeni* and *Opuntia spinosior* are present and only one each of these species was included in the plot selected for this work. The bushes on area TB show very good growth. They are more uniform in height, 4 to 5 feet, and in diameter than those of any of the other areas. The soil on this area is very deep and has been derived from the Tucson mountains, which are of volcanic origin. An excavation to a depth of 4 feet revealed no caliche layer and if a hardpan layer is present at a greater depth it is doubtful whether the Larrea roots come into contact with it.

Area LI or "Larrea Island" is the name applied by the author to an area in the Avra Valley approximately three acres in extent which is isolated from all other creosote areas, except for a smaller "island" 300 yards distant, by a very gently sloping grassland area 2 miles in extent along the shortest radius. Area LI is 5 miles indirectly west from TB. That this creosote "island" is a remnant of a more continuous stand is indicated by the fact that there is practically no reproduction on the area and there is no indication on the margin of the area that the Larrea is spreading. All of the bushes are relatively old, as indicated by their size, most of them having reached a height of 5 to 6 feet in most cases and having acquired a considerable quantity of dead branches. The soil on this area is probably of the same origin as that at area TB, although it is possible that some of it may have been brought in from greater distances. It has a greater sand content than soil from the other areas and an excavation to a depth of 4 feet revealed no caliche layer. This area is subject to light grazing and although stock do not eat mature Larrea it is quite possible that they may clip off the young seedlings along with other vegetation and, of course, some of the seedlings, if any start, may be trampled down. These factors, however, are not considered to be of sufficient magnitude to account for the almost total lack of new plants on the area. During the period of summer rains a very heavy covering of grass and summer annuals springs up on area LI and the surrounding grassland and

the winter rains bring numerous winter annuals into active growth. Except at these two periods of the year Larrea is the only active plant of importance on the area.

Within the plots staked out on each of the 4 creosote areas described above, two representative *Larrea tridentata* bushes were marked for study. The majority of the data obtained for the areas, by the methods used, center around these selected bushes. Beginning on March 8, 1931 and continuing at intervals until August 29, 1931, collections of leaves and adjacent small twigs were made from each of the eight chosen bushes and soil samples were taken at the same time for determinations of moisture content and total soluble salt content. The interval between collections varied from 6 to 17 days, depending upon the weather and other conditions. Most of the collections, however, were made at intervals of one week.

The methods followed in collecting and preparing the leaf material for the cryoscopic determinations and the method used in determining the osmotic values were in general the same as those reported by Walter (1931). Certain changes were found convenient and certain variations necessary to adapt them to studies of plants of the creosote bush type.

METHOD OF COLLECTING AND KILLING LEAF AND TWIG SAMPLES

The leaf and twig samples were collected in short glass vessels, test tube-like in shape, and closed by cork stoppers. The manner of taking the samples was to strip off the leaves and small twigs by grasping the foliage with the right hand and pulling upward and outward at proportionate intervals while slowly moving completely around the bush. One leaf sample was taken from each bush at each collection. The glass vessels were approximately one and one-half inches in diameter and had a capacity of approximately 75 milliliters. These were packed full of material, corked and then placed in a close-fitting aluminum canister which had a screw top.

The tissues were killed by placing the aluminum canisters containing the leaf samples in a vessel with moderately tight-fitting cover and by heating the material for 30 minutes in an atmosphere of boiling water. Water was placed about the sample cans up to one-third of their height and was brought to the boiling point as rapidly as possible. The entrance of water into the sample cans is readily detected by the presence of moisture in the soft dry tissue paper which is placed in the bottom of each aluminum canister. This small quantity of tissue paper also serves as a shock absorber for the glass vessel and serves to make the cork of the vessel fit tightly against the screw top of the canister, thus preventing the cork from being dislodged or loosened by pressure developed within the glass vessel during the heating. Following the heating process the samples were cooled to room temperature and then placed under refrigeration.

METHOD OF EXTRACTING THE SAP

A Fred S. Carver hydraulic laboratory press was used for expressing the plant juices with a pressure of 14,000 pounds per square inch. This press gave very satisfactory results and was relatively easy and rapid to operate. The samples under refrigeration were allowed to come to room temperature before they were placed in the press. The material was then removed from the sampling jar with forceps and wrapped in a heavy muslin cloth about 15 centimeters square. The soiled cloths resulting from a series of pressings were boiled, rinsed, and dried before being used again.

Since there is no extraction chamber on the market suitable for expressing juices from biological material for cryoscopic determinations one was made from a good grade of stainless steel. This chamber differed somewhat from the press vessel described by Walter (1931) and the illustration, Figure 1,

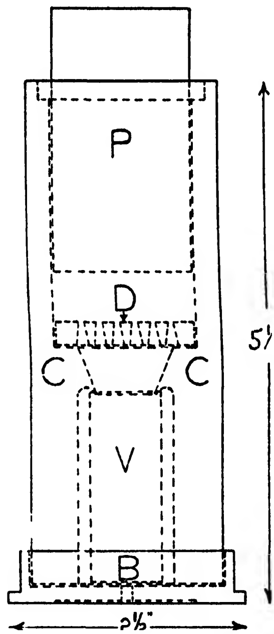

FIG. 1. Plant sap extraction chamber consisting of a main cylinder (C), a plunger (P), a perforated disc (D), a glass vial (V), and a brass base (B). Parts C, P, and D are of stainless steel.

shows the details of its construction. The addition of a groove cut around the inside wall of the main cylinder one inch from the top as described by Meyer (1929) would help prevent the upward movement of sap beyond that point. In this work the cell sap was squeezed directly into small vials in which it was stored until wanted for the cryoscopic determinations.

The order of assembling the extraction chamber is as follows: the per-

forated disc is placed in the bottom of the upper end of the main cylinder, a piece of clean muslin 1½ inches wide and 5 to 6 inches long is folded over two or three times and placed on top of the disc, the plant material wrapped in muslin as described above is then inserted in the upper end of the cylinder followed by the plunger. The insertion of the glass vial into the lower end of the cylinder and the mounting of the whole upon the brass base completes the operation. This assemblage is then placed upon the movable stage of the press and pressure is applied.

It was found quite essential to place two or three thicknesses of cloth over the perforated disc to prevent solid material from being pressed through. Although the osmotic value determinations would probably not be affected by the presence of solid materials in the sap, as shown by Hibbard and Harrington (1916) and others, the inconvenience and time consumed in cleaning the material out of the holes in the disc between each pressing warrants any precautions which can be taken to retain all of the solid material in the upper portion of the cylinder.

The use of such a high pressure as 14,000 pounds would not have been necessary during the rainy season but during the arid foresummer it was quite difficult to obtain, even at that pressure, sufficient sap from a single collecting jar full of material to make a freezing point determination. When the material was quite dry the limit of its compressibility was quickly reached and the pressure indicator hand on the manometer remained stationary. As the material became more nearly saturated, with the advent of the rainy season, considerable time was required for the limit to be reached and since such a high initial pressure was being used it was thought unnecessary to continue the application of pressure until the indicator remained stationary, as would be advisable if a lower pressure were applied. Accordingly, a pressure of 14,000 pounds was applied and the extraction chamber was not removed from the press until either the pressure had dropped below 6,000 pounds, or, if the pressure did not decrease, until a period of 30 minutes had elapsed to permit the drainage of the sap into the vial. The vial containing the plant juice was removed from the cylinder, stoppered, and placed immediately in an electric refrigerator.

DETERMINATION OF THE FREEZING POINT

The majority of the cryoscopic work done in America has been accomplished with either a Beckmann or a Heidenhain thermometer. With these instruments it is necessary to have at least 15 milliliters of plant sap for a determination. When, however, a so-called microthermometer, such as a Drucker-Burian, is used, only 1.5 to 2 milliliters of juice is necessary. This feature is a distinct advantage in arid regions, especially when non-succulent plants are being studied. Also it is an advantage when numerous samples are to be collected from the same plant over a period of time, since only

relatively small amounts of material need be removed from the plant at any one time. Both of these factors were important in the present work and therefore a Drucker-Burian microthermometer, made by Robert Goetze, Leipzig, was used. Walter (1931) presents a good illustration and complete description of this equipment.

The expressed sap samples under refrigeration were allowed to come to room temperature before their freezing-point depressions were determined. The quantity of sap used must be sufficient to cover the thermometer to a height about 2 mm. above the mercury bulb.

After the freezing vessel and cell sap had been pre-cooled directly in the ice-salt mixture they were quickly transferred to the air jacket which had previously been suspended in the ice-brine mixture. The freezing vessel was held firmly in place in the air vessel by means of a cork gasket and care was exercised not to have the freezing vessel come into direct contact with the air vessel since this would lead to an unequal cooling of the sap. The solution to be tested was stirred constantly throughout the determination and the freezing mixture was also agitated from time to time.

When the desired degree of undercooling was attained a glass seeding capillary containing a particle of frozen distilled water was quickly introduced into the sap sample, immediately withdrawn, and the sap rapidly stirred. The seeding capillary may be successfully replaced by a length of platinum wire with a cork on the upper end to insulate against the heat of the hand. The highest point reached by the mercury is noted and for the first determination on a sample this reading was taken as the approximate freezing point, since the amount of undercooling was so great. This approximate value enables one to estimate very closely where the true freezing point will be and therefore the point at which the precooling should be stopped for an undercooling of one degree.

In the Drucker-Burian thermometer the scale is so short that it is impossible with most solutions to determine the total amount of undercooling which would occur if the solution were not disturbed, since the mercury would go below the scale. Therefore, it is necessary to stop the undercooling by seeding the solution with a crystal of ice as described above and the most convenient place to stop the undercooling is one degree centigrade below the actual freezing point, since this factor may then be disregarded in the correction formula which will be noted below.

Following the initial supercooling and freezing point determination the freezing tube is removed from the air jacket and the contents melted by holding in the hands and stirring gently. When all ice crystals have disappeared from the sample the freezing tube is again put directly into the ice-salt mixture for precooling. As soon as the mercury has fallen a little below the estimated freezing point the freezing vessel is transferred to the air jacket

for the remainder of the determination. At a temperature approximately 0.3° C. above the temperature at which the undercooling should be stopped, the solution is seeded with a crystal of ice. This anticipation of the undercooling temperature is necessary since the temperature invariably drops very suddenly about 0.3° C. immediately after the seeding and before it rises to the freezing point. In this work the process of determining the freezing point was repeated with each sample until two readings with a difference no greater than 0.005° C. were obtained.

It was found quite necessary to work at the same speed, in all determinations, especially in stirring. Otherwise the rapid rising and falling of the platinum stirrer will influence the temperature of the mercury filament unequally and inject error into the results. Considerable practice is necessary to acquire the proper technique and to obtain dependable results. The best indication of accurate work is the obtaining of two successive identical readings.

The determination of the zero point on the thermometer, which is the freezing point of distilled water, follows the same procedure as that given above for the plant sap.

CALCULATION OF THE OSMOTIC VALUE

The osmotic values are here reported in atmospheres of pressure. Variations in the osmotic values are more apparent when the values are expressed in atmospheres rather than in degrees of depression, since the units are larger. The correct values for depression of the freezing point were obtained by using the correction formula of Lewis (1908).

For converting the corrected depression of the freezing point readings into osmotic values expressed in atmospheres of pressure the tables of Harris and Gortner (1914) and Harris (1915) were used. Since according to Harris and Gortner, the first differences Xo.1 may be taken as 0.012, the pressures when Δ is read to thousandths of a degree may be readily determined. A detachable reading lens or a hand-lens is necessary for reading the thermometer to the third decimal point.

SOIL MOISTURE DETERMINATIONS AND RAINFALL RECORDS

The soil samples for the moisture determinations were collected in wide-mouthed, pint Mason jars at the same time that the leaf samples were taken and approximately one meter from the center of the crown of the bush. The jars were filled almost full and the moisture content was found on the basis of the percentage of the dry weight of the soil after it had been dried to constant weight at 103 to 105° C. Each sample consisted of approximately 360 to 700 grams of oven-dry soil. One sample was taken from the vicinity of each of the selected bushes on every leaf-collection tour, thus making a total of two samples from each area per collection.

Approximately 15 cm. was chosen as the most suitable depth at which to take the samples for two reasons; first, because on areas CB and CP it is impossible to dig much deeper without great labor, and second, because it was thought that samples taken at this depth would give a good indication of the moisture conditions with which young Larrea seedlings would come into contact and that they would give a better index to the fluctuations in the soil moisture than samples taken at shallower or at greater depths.

The rainfall records were obtained by means of rain gauges, one of which was placed on each area. These gauges were quite simple and consisted merely of a quart Mason jar, a one-hole cork stopper to fit the jar, and a large galvanized iron funnel. A quantity of a good grade of motor oil was placed in each jar to prevent the evaporation of the water between readings.

SOLUBLE SALT DETERMINATIONS

Periodic determinations of the total soluble salt content of the soils of the experimental areas were made in conjunction with the soil moisture determinations by means of the modified Wheatstone bridge as developed in the soil physics laboratory of the U. S. Bureau of Soils. A description of the electrolytic bridge and instructions for its proper manipulation have been published in convenient form by Davis (1927). He also gives tables from which the total soluble salts in solution at 60° F. may be read directly in parts per million for resistances from 68 ohms to 10,200 ohms.

MECHANICAL ANALYSIS OF SOILS

The hydrometer method of Bouyoucos (1928) was used in making the mechanical analyses of the soils from the respective areas. This method makes use of Stokes' law and hydrometer readings taken at given intervals of time. Bouyoucos found that the determinations made by his method agreed very closely with those obtained by the mechanical analysis method except in the case of the finer silt. Due to the fact that the finer silt has more of the characteristics of clay, the hydrometer method classes it with the clay while the mechanical analysis method places it with the coarse silt. For the type of work presented here the hydrometer method is sufficiently accurate, especially, since it is less complicated and requires less experience for proper manipulation than does the more time-consuming older method of mechanical analysis.

CHEMICAL ANALYSIS OF SOILS

The chemical analyses of soils from the four creosote areas and another area about 100 meters from LI on which no Larrea was present, were made in the agricultural chemistry department of the University of Arizona under the direction of Professor R. A. Greene. A 1 to 5 soil extract was prepared by shaking 100 grams of soil with 500 milliliters of water and filtering it

through a Pasteur-Chamberlin filter. The calcium and magnesium were determined by titration with standard soap solution and the chlorides by titration with standard silver nitrate. The amount of sulphates present was found turbimetrically. Carbonates and bicarbonates were determined by titrating the soil extract with fiftieth normal sulphuric acid using phenolphthalein and methyl orange respectively as indicators. The quantity of sodium was calculated by the difference between the reacting values while the nitrates were determined colorometrically by the phenoldisulphonic method. These methods have been adapted or developed for use with southwestern soils by the agricultural chemistry department of the University of Arizona.

The soil samples for these analyses were all collected on the same day and each one was designed to be representative of the top six to eight inches of soil at the respective locations. Two samples were collected on each area, one from a high spot and one from a low place there being as much as one foot difference in elevation in some cases. A chemical analysis of the soil as described above was thought important in determining the uniformity or lack of uniformity between the Larrea habitats in respect to the chemical composition of the substrate.

ASH ANALYSIS OF PLANTS

The calcium and magnesium content of the plants growing on the various areas was determined in order to discover whether the presence or absence of caliche near the surface has any appreciable effect upon the amounts of calcium and magnesium absorbed by the plants. There is evidence that calcium compounds have strong imbibitional properties and that the drought resistance of a plant is at least partly dependent upon their formation, since they serve to bind water within the tissues. Also it was desired to determine whether any marked difference in the content of these two ions was reflected in the seasonal changes in the sap concentrations of the plants.

The plant material for these analyses consisted of root and top potions of ten plants from each area. The roots and tops were kept separate. The material was prepared for analysis according to the methods of the Association of Official Agricultural Chemists (1924 revision), page 39. For determining calcium the tentative volumetric method given in section 6, page 41 of the above publication was followed and the tentative gravimetric method for magnesium given in the succeeding section, number 7, page 42, was adopted up to the point where the sample is ignited and weighed as magnesium pyrophosphate. For the final determination of the magnesium the volumetric method of Handy as given in Scott (1917), was used.

DIURNAL VARIATIONS IN OSMOTIC VALUE

In order to determine what influence the time of collection of the leaf and twig samples might have on the osmotic values found for the various collec-

tions, samples were taken at two, three, and four-hour intervals, depending upon the time of day, for a period of fifty-two hours. Two Larrea bushes, A and B, located near the laboratory, were selected for this experiment. Bush A was a large one located in a pocket of soil surrounded by very large rocks which are thought to form a basin for moisture and to play an important rôle in its conservation, since this bush appeared to be in very good vegetative condition at all seasons of the year. Bush B was smaller than A but may be described as a representative bush. It was located on a well-drained slope about fifty yards from Bush A. The leaves of B were relatively small as compared to those of A but it too was considered to be in good vegetative vigor. Bush B was representative of the average creosote bush of the bajadas, judging from its general appearance, and bush A was representative of the large, tall, vigorous type of bush found in low spots where surface waters collect.

Presentation and Discussion of Data

RELIABILITY OF THE METHOD OF SAMPLING

A short experiment was designed to determine the reliability of the method of taking the leaf samples as previously described. Four samples were collected from the same Larrea bush within a period of fifteen minutes. These samples were then treated in the manners described above and yielded the following values for the expressed saps:

Sample	Δ	Ov
9x	1.965	23.620
10x	1.916	23.032
11x	1.896	22.796
12x	1.935	23.260

The greatest difference between these values is 0.069° C., or 0.832 atmospheres. This difference is somewhat greater than is desirable, however, since the values for samples 10 x, 11 x, and 12 x are relatively close together the greatest difference here being only 0.039° C. or 0.470 atmospheres, we may attribute the fact that sample 9 x gave such a high value, at least, in part, to some error in the determination rather than entirely to erratic sampling.

Two other instances may be cited in this connection. Duplicate leaf samples were collected in rapid succession from two Larrea bushes. One set of samples yielded osmotic values of 22.144 and 21.724 atmospheres and the other gave values of 28.340 and 27.990 atmospheres. From these data it is evident that differences in osmotic values of as much as 0.500 atmospheres may be accounted for as a variation in the uniformity of sampling when working with Larrea or a similar plant.

SEASONAL VARIATIONS IN OSMOTIC VALUES

The variations in the osmotic values of the sap of leaves and small twigs of *Larrea tridentata* growing on the four experimental areas are presented in Figure 2. The average of the osmotic values found for each collection

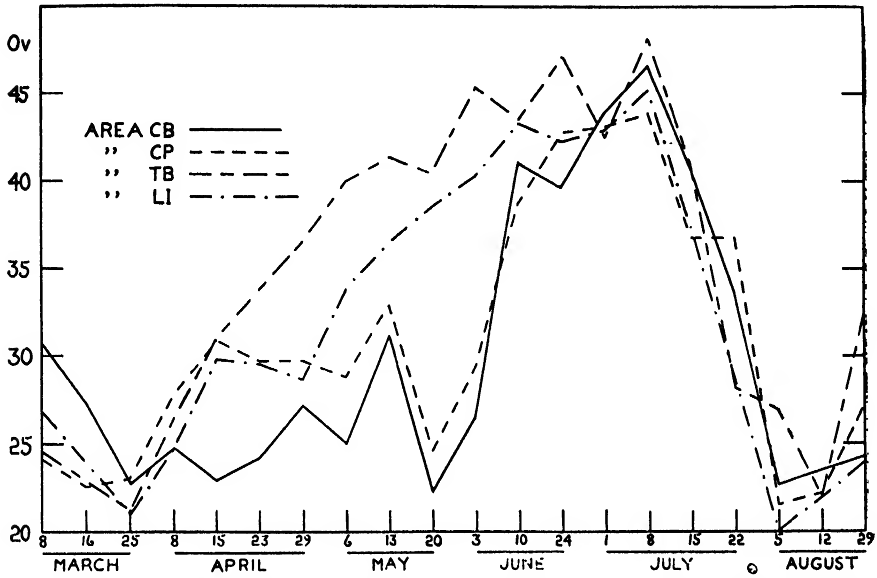

FIG. 2. Average osmotic values of the sap from leaves and small twigs of *Larrea tridentata*.

from two creosote bushes on each of the areas studied are used rather than the separate values found for all of the bushes. While it is not desirable to attempt to establish fundamental facts upon studies of such a limited number of individuals, numerous determinations on the same individuals over a considerable period of time serve to offset this weakness. Moreover, on two occasions during the course of these studies samples were collected from a considerable number of individuals on each area for the purpose of determining the individual variations in the osmotic values on each area at a given time. The results of these tests will be reported later in this paper.

Figure 2 reveals several facts concerning the seasonal variations in the osmotic values of the creosote bush. The highest average osmotic values for all four of the areas were found for the collections of July 8th. The lowest average osmotic values for areas CB and TB occurred on March 25th and the lowest values for CP and LI on August 5th. Moreover, on March 25th, July 1st and August 12th the osmotic values for all four areas were closer together than at any other time during the season. These facts indicate therefore that the greatest response of these plants to environmental conditions as indicated by changes in the concentration of the cell sap takes place

in approximately the same length of time regardless of variations in the environmental factors during the period between the occurrence of maximum and minimum sap concentrations. Also it will be noticed that the osmotic values become more nearly equal as the maximum and minimum values are approached. This is due mainly to the fact that as the limits of desiccation or saturation are reached the effect exerted on the concentration of the sap by the volume and activity of the root system is minimized.

The minimum osmotic values are more nearly equal for all areas than are the maximum values. This may be taken as an indication that the qualities of a creosote bush which make for drought resistance are not present in equal degrees in the plants on the different areas. If the degree of drought resistance is chiefly dependent upon the quantity of hydrophilic colloids or other substances which may bind water within the plant, then plants which contain different quantities of such substances will possess different osmotic values, especially as the tissues become drier and drier.

The sap concentrations of leaf and twig material collected on areas CB and CP were more constant than those from areas TB and LI. From the locations of the areas given above it will be recalled that areas CB and CP and areas TB and LI are much closer to each other geographically than they are to any of the other areas. Therefore, the environmental factors affecting the plants of these two pairs of creosote areas would be expected to be and, as will be shown later, are more nearly equal than those for any other combination of locations studied. This also explains the closer equality of values from areas CB and CP and from areas TB and LI throughout the season than from any other two areas.

The curves for all of the Larrea areas, produced by plotting their osmotic values on the same scale, are quite similar. In general, they resemble the "normal distribution" curve. The curves for TB and LI rise more gradually than those for CB and CP, probably due to differences in the climatic factors, but the curves all descend together and somewhat more abruptly than they rose, as the summer rainy season advances.

A summary of the seasonal range of osmotic values for the individual creosote bushes and the individual areas studied is given in Table 1 for the period March 8 to August 29, 1931.

TABLE 1. Seasonal range of osmotic values arranged in descending order.

Individual Bushes	Max. Ov.	Min. Ov.	Range of Variation
TB_5	50.472	21.376	29.096 atm.
LI_7	48.644	20.368	28.276 "
TB_6	49.006	21.016	27.990 "
CB_1	47.262	22.192	25.070 "
CB_2	46.456	21.484	24.972 "
CP_3	45.784	22.240	23.544 "
LI_8	42.082	19.828	22.254 "
CP_4	42.646	20.656	21.990 "
Average	46.544	21.145	25.399

Individual Areas	Max. Ov.	Min. Ov.	Range of Variation
TB	48.422	21.196	27.226
LI	45.363	20.098	25.265
CB	46.859	22.408	24.451
CP	44.155	21.664	22.491

Except in the case of bushes LI_7 and LI_8 the bushes from the areas form a very regular series with the succession TB_5, TB_6, CB_1, CB_2, CP_3 and CP_4 when they are arranged in the descending order of the range of variation of their osmotic values. This affords evidence that there is a fairly characteristic range of osmotic values for this plant for each particular habitat in which it grows and that this range is practically the same for all Larrea plants growing in any given habitat. Bush LI_8 is the only one studied which does not fall in line with this evidence. However, in spite of the fact that its range is next to the lowest in the series, yet area LI is able to hold second highest place in the seasonal range of osmotic values because the seasonal range for bush LI_7 was sufficiently large to keep the average up. The great difference between the values for LI_7 and LI_8 are not surprising. As stated above, the creosote plants on the "Larrea Island" are apparently merely holding their own against fatally adverse conditions. It is to be expected, therefore, that the principle of the survival of the fittest will be most operative in this habitat and that the individual differences between plants will be more apparent than they would be under more favorable conditions of growth.

The arrangement of the four areas in a series in the descending order of their seasonal range of osmotic values corresponds exactly to a classification of the areas based on the desirability of the habitats for the growth of creosote as indicated by the appearance of the bushes and the amount of vegetative growth and reproduction present. Starting with the best habitat and ending with the poorest, the classification of the areas would be TB, LI, CB, and CP. These facts would lead one to believe that a wide range of variation in osmotic value is favorable to the plant but it may be argued that since the greatest differences are in the maximum values, the conditions of drought did not become equally severe on all of the areas, and had the dry period continued for a greater length of time, the ranges of variation would have been closer together, if not equal. The writer judges, however, that a continuation of climatic conditions which would raise the maximum osmotic value of one bush would also increase that value of the plants on all of the areas, and in order for all of the bushes to reach the same maximum value a difference in rate of change or a difference in the "osmotic inertia" of Larrea such as suggested by Walter (1929) for plants of different species, would have to be operative. The curves in Figure 2 do not give support to this theory when it is applied to plants of Larrea, since during the periods when conditions were more nearly uniform on all of the areas, the osmotic values quickly approached each other and the response was quite uniform as long as conditions remained approximately equal.

The osmotic values reported by Whitfield (1932), for *Artemisia californica* appear to support the observation that plants of a given species which experience the widest range of osmotic values also exhibit the best growth. Plants of this species from the sand dunes where its growth is best had a range of 11.2 atmospheres, those from the coastal chaparral 3.8 atmospheres, and specimens from the coastal sagebrush associations 0.8 atmospheres. Samples were collected at only two seasons and it is possible that the extreme values were not obtained. The limited data are in line, however, with the findings for the creosote bush.

OSMOTIC VALUES OF LARREA AS INFLUENCED BY SOIL MOISTURE AND RAINFALL

In Figures 3 and 4 a graphic comparison is presented of the percentages of soil moisture with the osmotic values and with the precipitation in inches. The total rainfall on the different areas during the period of the investigation

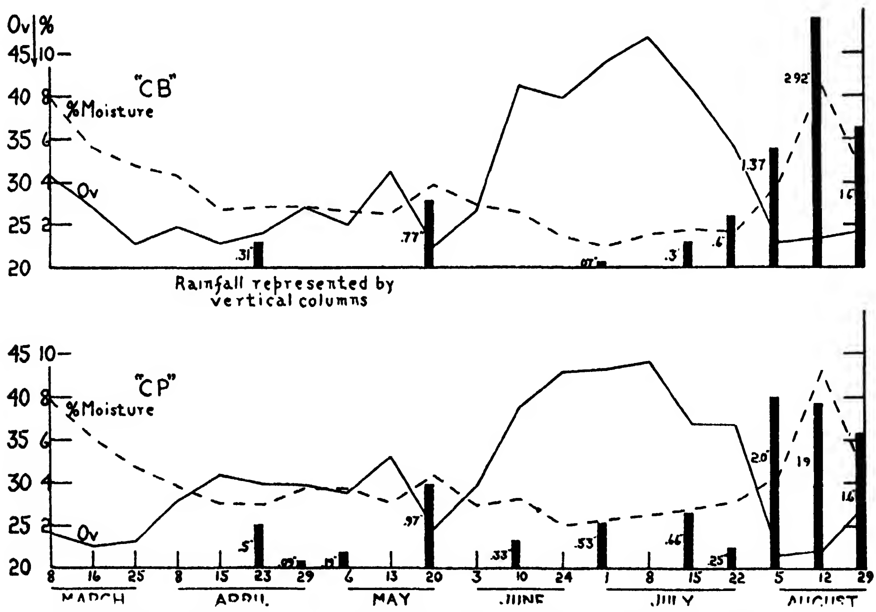

FIG. 3. Osmotic values of Larrea on areas CB (above) and CP (below) in relation to soil moisture and rainfall. Total rainfall between readings is indicated in inches by the figures adjacent to the black columns.

was as follows: CB, 8.00 inches; CP, 9.04 inches; TB, 6.71 inches; and LI, 6.70 inches. The distribution of this precipitation is shown by the location of the vertical columns on the graphs. From the position and height of these columns it is apparent that the rainfall pattern for all four areas was quite similar. Area CP, which received the most rain, had precipitation during three periods when the other areas received none. This indicates that

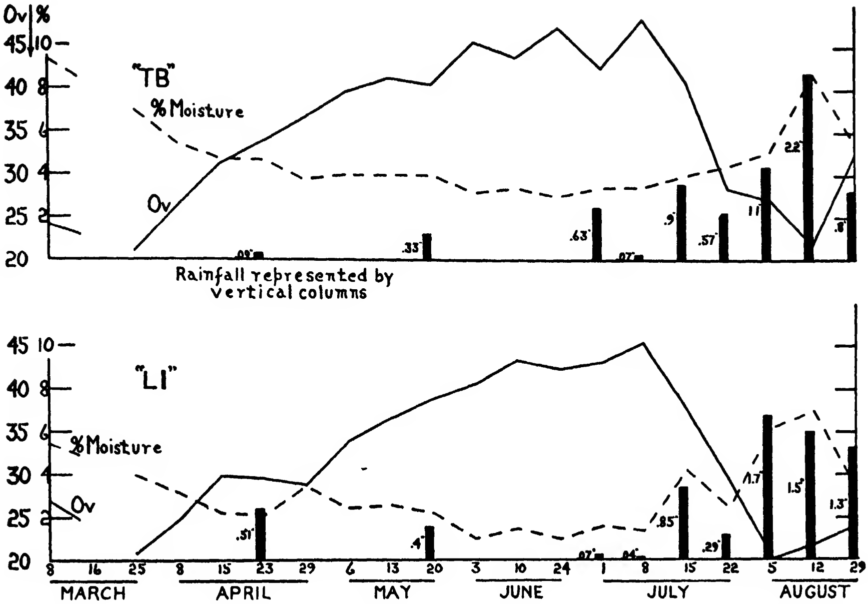

FIG. 4. Osmotic values of Larrea on areas TB (above) and LI (below) in relation to soil moisture and rainfall. Total rainfall between readings is indicated in inches by the figures adjacent to the black columns.

the larger total for this area may be attributed to a greater number of separate showers rather than to heavier rainfall on the same days in which all of the areas received moisture. Only one of these three periods; namely, that from June 3 to June 10 yielded sufficient moisture to be of much aid or importance to the vegetation. The precipitation for this interval was 0.33 inch while for the other two periods it was only 0.09 and 0.19 inch. The fact that area CP received rain over a greater period of time may have been one factor in preventing the Ov from rising as early or as high as those for areas TB and LI; however, it is interesting to note that the fall of 0.33 inch of rain on area CP did not prevent the osmotic concentration from beginning its rise toward the seasonal peak on the same day as it did for area CB although the sap concentration did not increase quite as much as it did for CB. It seems, therefore, that factors other than rainfall alone were influencing the change in osmotic value.

The season of summer rains may be considered as beginning on July 1st for areas CP and TB but not until July 15th for areas CB and LI. All of the osmotic values, however, show a relatively equal decrease on the same day, July 8th, regardless of the amount of precipitation. This again indicates that some other factor was more important than the amount of rainfall.

Turning now to a consideration of the percentage of soil moisture at a depth of approximately 15 centimeters, in the various habitats throughout

the season, a close correlation is seen to exist between it and the osmotic value of the expressed sap of leaves and twigs of Larrea. An increase in the moisture content produced a decrease in the osmotic value in practically every instance, especially if the change in soil moisture content was as much as 0.25 per cent. The average of the moisture contents of the soil in the respective areas, as determined at intervals during the period of this investigation, was 3.5 per cent for CB, 4.0 per cent for CP, 4.7 per cent for TB and 3.0 per cent for LI. The low value for LI is probably partly attributable to the fact that the soil of this area contained a larger percentage of sand than did any of the other soils and therefore its water-holding capacity was less and the moisture evaporated more readily from the first few inches and also penetrated deeper than on the other areas. The moisture content of soil samples taken at about 25 centimeters on area LI would probably have been more nearly equal to the moisture content of the 15 centimeter samples from the other areas. Nevertheless, area TB which had the highest seasonal average moisture content of the soil also has a soil which is quite sandy, as was shown by the results of the mechanical analysis. Regardless of the fact that area TB had the highest average percentage moisture and area LI the lowest, yet the sap concentration of both of these areas began to rise toward the seasonal peak on the same day, March 25th, and suffered only minor decreases until the maximum osmotic value for the season was reached. On the other hand, areas CB and CP did not show a definite continuous rise toward the maximum concentration of the sap of leaves and twigs of Larrea growing on them until May 20th. Then the plant sap from both areas exhibited a definite increase toward the seasonal peak of osmotic values. Soil samples from areas CB and CP yielded average percentage moisture contents for the season which are intermediate when compared with the corresponding values found for the other two habitats. The writer believes that differences in response were not due primarily to differences in rainfall on the areas or to basic differences within the plants on the four areas but rather to the presence of the layer or layers of caliche in the soil of areas CB and CP which served to prevent rapid movement and evaporation of moisture which had penetrated through cracks and crevices to the soil beneath the caliche. The roots of the plants on these areas had also penetrated the caliche more or less successfully and were drawing upon the moisture of the soil beneath, thus prolonging the period of low sap concentration eight weeks over that of areas TB and LI. It is true that areas CB and CP received more moisture from the rains which fell about April 23rd and May 20th than did either of the other two habitats. But, in view of the fact that the sap concentrations began to rise immediately following the precipitation of over 1.5 inches around May 20th, these rains evidently had little effect on the vegetation and it was the moisture conserved by the caliche which was the chief factor in keeping the osmotic values low, up to and including that time.

It is interesting to note that the highest osmotic concentration for each of the areas occurred at least one week, and in most cases, two weeks after the lowest moisture content of the soil at a depth of 15 centimeters. This lag is to be expected since the soil at 15 centimeters dries out much more rapidly than does the soil which surrounds the bulk of the root system at greater depths. However, the "osmotic inertia," of the plants may also be a factor here, and if so, it is evident that the rate of change is approximately equal on all areas.

Except in the case of area TB the lowest sap concentrations were found in the samples collected one week before the highest percentage soil moisture occurred. If we eliminate the determinations of soil moisture for area TB for the period prior to April 8th which is, moreover, not complete, then the highest soil moisture for all of the areas occurred on the same day, August 12th, which was in the midst of the summer rainy season. The weather during the period between August 5th and August 12th, was wet and cloudy and therefore the top soil did not have an opportunity to dry out as it had previously and besides it was becoming saturated. This accounts for the high moisture content on this day at 15 centimeters. The plants had received sufficient moisture by August 5th to produce the lowest sap concentration except in the case of those bushes on area TB, where, however, the lowest osmotic value was found on August 12th. This again emphasizes the fact that the response of the plants on all of the areas to soil moisture is, for all practical purposes, equal when the response is measured in terms of osmotic value.

While the number of determinations of the moisture equivalent and wilting coefficient of these soils is very limited it is reported here because it proved to be very interesting and to have a significant bearing upon the moisture relations of Larrea. The method of Briggs and McLane (1907) was used in making the moisture equivalent determinations. The average moisture equivalents of two determinations for each area in per cent were as follows: CB, 11.09; CP, 12.71; TB, 15.74; and LI, 8.75. The formula of Briggs and Shantz (1912) was used for calculating the wilting coefficient from the moisture equivalent for the respective soils. The wilting coefficients in per cent are as follows: CB, 6.03; CP, 6.91; TB, 8.55; and LI, 4.75.

Comparing these calculated wilting coefficients with the average soil moisture determinations an interesting fact is brought to light. In only two collections of soil from CB, CP, and TB and in three collections from area LI did the percentage of soil moisture exceed the wilting coefficients for the respective soils. These samples were taken on March 8th and August 12th for all the areas and also on August 5th for area LI. The soils collected on all other dates during the period of this investigation contained a percentage of moisture below the wilting coefficient. In the case of area TB this deficit

amounted to 5.5 per cent on June 24th. All of the maximum deficits occurred on the same date for all areas except CB, where it occurred one week later.

That Larrea can survive under these conditions is self evident. In fact, the area (TB), on which the creosote bush was conceded to be making the most successful growth, showed the greatest moisture deficit at 15 centimeters. What the moisture conditions were below this depth are not known. Breazeale (1930) has determined experimentally that some plants may absorb moisture from any soil horizon where water is available, for example, a subsoil, and transport this moisture to another horizon, where moisture is scarce, for example, the surface soil. Here the plant may "exude" this water; the water may in turn dissolve and absorb certain amounts of nutrient material. He used wheat and corn in his experiments. Considerable research will be necessary to determine whether this holds for Larrea. That Larrea must produce root hairs in the upper layers of soil which are either active all the time or are quickly brought into an active state is indicated by the ready response of the creosote bush to rains which penetrate the soil to a depth of only two to four inches.

Another interesting consideration connected with the above data is the relationship which the moisture content of the upper layer of soil may bear to reproduction of Larrea. It is difficult to understand how young seedlings can become established in soil which, during a very great part of the time, has a moisture content below the calculated wilting coefficient for that soil. Magistad and Breazeale (1929) have pointed out that roots of cactus (Opuntia) will grow into soil, and will live and elongate in soil in which the moisture content is kept at the wilting percentage or even in an air-dry condition. The plant will continue to live under such conditions only so long as it contains sufficient moisture to meet its metabolic needs and to keep the moisture content of the soil atmosphere immediately surrounding the roots in equilibrium with the moisture content of the roots. It is known that cactus joints are readily rooted by placing them in air-dry soil or sand and allowing them to stand without water until the root system is established. The soil in such cases serves primarily as an insulation against the rapid diffusion of the water vapor given off from the underground parts of the plants. The resulting increase in the humidity of the atmosphere of the soil stimulates the growth processes of the plant and roots are produced. These facts are readily understood for plants or plant parts which possess large water-storing capacities. However, such facts have not been established for seedlings of these plants or for a non-succulent, woody perennial like Larrea. In general it may be stated that plants, especially mesophytes, cannot reduce the moisture content of soil below the calculated wilting percentage except, perhaps, under conditions where there is a sufficient water supply in the lower levels of soil and where enough roots penetrate therein to furnish the bulk of the water necessary to replace that lost from the leaves.

The possibility is great, therefore, that the low moisture content of the upper layers of soil may play an important rôle in bringing about the scanty reproduction of the creosote bush. A typical creosote area is not densely populated by Larrea and usually the surface of the soil is relatively free from vegetation. The first 30 cm. of soil is quite well permeated by roots and there is no doubt some competition for moisture. However, there cannot be much competition in soil in which the moisture content is below the wilting percentage nearly all of the time. It seems probable, therefore, that seedlings of Larrea are able to survive in soil in which the moisture content is below the calculated wilting coefficient and is also below the percentage at which many plants would permanently wilt. If this is not true, then new creosote bushes become established only during periods in which the rainy season is sufficiently extensive and intensive to raise the moisture content of the soil above the wilting percentage long enough to give the seedling roots an opportunity to become established at a depth where the moisture content is adequate throughout the year. The greatest number of young creosote bushes per given unit area are almost invariably found where the soil has been disturbed as, for example, along roadways and around excavations where scrapers and other implements have loosened and piled up the soil. This indicates that seed germination and seedling development are aided or are made possible by covering the seeds to prevent rapid desiccation and by loosening the soil to facilitate the penetration of the roots. Moisture also penetrates more readily into soil which has been disturbed and there is less lost as "runoff." The rain that falls is therefore more effective in maintaining the moisture content of the soil.

OSMOTIC VALUES OF LARREA IN RELATION TO THE TOTAL SOLUBLE SALT CONTENT OF THE SOIL

As would be expected, there is apparently no correlation between the total soluble salt content of the soil at 15 centimeters and the osmotic value of the sap of leaves and twigs of Larrea growing thereon. The greatest variation in the determinations was found on area TB where it amounted to 115 parts per million; a change of only 0.0115 per cent. This amount of change is not of sufficient magnitude to be of any importance to the life of the plant coming into contact with the soil solution. The variation at greater depths in the region of the main bulk of the roots was probably even less than at 15 centimeters where the salts are more subject to leaching.

The seasonal average soluble salt concentration in parts per million for the soils of the various habitats were 206 for TB, 145 for CB, 139 for CP, and 102 for LI. The difference between the highest and lowest of these values, 104 p.p.m., might be important in connection with reproduction since it is the salt concentration at a depth of around 15 cm. with which the young seedlings first come in contact. An area with a relatively low salt concen-

tration would be most favorable for young plants. However, if the areas are arranged in the descending order as regards the presence of young plants on them, they would be in the same order as when arranged in a series of decreasing soluble salt content; namely, TB, CB, CP, and LI.

Total soluble salt determinations made on the same soils in the agricultural chemistry department of the University of Arizona were considerably higher than those made with the "soil bridge." The values obtained at the chemistry department were for TB, 292 p.p.m.; for CP, 287 p.p.m.; for LI, 278 p.p.m.; and for CB, 248 p.p.m. These concentrations are practically equal since there was only 44 p.p.m. difference between the highest and the lowest values. Two samples taken about 100 meters from LI, where no creosote was growing, gave values of 155 and 269 p.p.m. or an average of 212 p.p.m. This average is lower than the lowest concentration of soluble salts found by the same method for the Larrea areas, although it is doubtful whether the difference is great enough to have any appreciable bearing on the absence of creosote on this area.

Summary of Seasonal Values

As an aid in comparing and visualizing the condition of osmotic value, soil moisture content, precipitation, and total soluble salt concentration existing on the various areas, a summary of seasonal or average values for the duration of this investigation is given in Table 2. These values show that area TB with the highest average moisture content and the highest average salt content also displayed the highest average osmotic value for sap of Larrea. This relationship did not hold for area LI which was characterized by the lowest average moisture content and soluble salt content, and likewise by the lowest total rainfall; yet the plants of this area gave the second highest value.

Table 2. Summary of seasonal values.

Type of Data	CB	CP	TB	LI	Arranged in descending order of values
Seasonal Average Ov per Collection......	30.125 atms.	30.906 atms.	35.475	32.490	TB-LI-CP-CB
Seasonal Average % Soil Moisture.......	3.5%	4.0%	4.7%	3.0%	TB-CP-CB-LI
Total Seasonal rainfall.	8 in.	9 in.	6.71 in.	6.70 in.	CP-CB-TB-LI
Seasonal Average Soluble Salt Content of Soils............	145 p.p.m.	139 p.p.m.	206 p.p.m.	102 p.p.m.	TB-CB-CP-LI

MECHANICAL ANALYSIS OF SOILS

The results of the mechanical analysis of the soil from the four creosote areas as determined by the hydrometer method of Bouyoucos are presented in Table 3. The classification of the soils is based on a diagram by Lyon and Buckman (1922). These figures show that the soil on area LI contains considerably more sand than does soil from any of the other areas. Therefore, its water holding capacity is less and it is subject to more rapid drying out than the other soils. This helps to explain the scarcity of reproduction on this area, since the soil may dry out so rapidly between rains that the young seedlings cannot become established well enough to survive the drought.

TABLE 3. Mechanical Analysis of Soils.

Area	*Sample*	*Per Cent Sand*	*Per Cent Silt*	*Per Cent Clay*	*Classification*
CB	1	74.36	12.0	13.64	Sandy loam
CB	2	72.87	10.8	16.33	Sandy loam
CP	3	72.47	13.0	14.53	Sandy loam
CP	4	66.57	13.5	19.93	Sandy loam
TB	5	57.50	14.0	28.50	Sandy clay
TB	6	62.15	12.5	25.35	Sandy clay
LI	7	85.36	5.5	9.14	Sand
LI	8	76.50	8.5	15.50	Sandy loam

CHEMICAL ANALYSIS OF SOILS FOR ALKALI SALT CONTENT

A chemical analysis of the soil from each of the four Larrea areas showed that there was very little difference between them in respect to chemical composition of the top 5 to 8 inches of soil, from which the samples were taken. Areas CB, CP, and TB were remarkably uniform in sodium, calcium, magnesium, chloride, bicarbonate, and nitrate content. Area LI was very similar to these except in the case of calcium, of which it contained none, and of sodium, of which it contained 20 p.p.m. more than the other areas.

The average values in parts per million for two chemical analyses for each area are presented in Table 4. In the last column the average pH value of four determinations on each soil are given.

TABLE 4. Chemical Analyses and pH of Soils.

Area	Na	Ca	Mg	Chlorides	Bicarbonates	Nitrates	pH
CB	41	15	12	10	183	11	7.62
CP	40	15	15	10	195	12	7.57
TB	41	15	15	10	201	10	7.74
LI	60	0	12	10	188	8	7.55

ASH ANALYSIS OF *Larrea tridentata*

The ash of the tops and roots of portions of ten Larrea plants from each area were analyzed for the calcium and magnesium content, in order to determine whether or not the presence or absence of caliche had any apparent relation to the amounts of these elements absorbed by the plants or whether there was any connection between the calcium and magnesium content and the variations in the sap concentrations of the plants. The results of these analyses are presented in Table 5.

TABLE 5. Calcium and Magnesium Content of *Larrea tridentata*.*

	Tops			Roots		
Area	CaO	MgO	Ratio Ca/Mg	CaO	MgO	Ratio Ca/Mg
	Per Cent	*Per Cent*		*Per Cent*	*Per Cent*	
CB	22.45	6.122	3.67	17.120	4.603	3.72
CP	16.86	4.775	3.66	8.069	3.004	2.67
TB	15.43	4.795	3.22	12.660	4.048	3.13
LI	24.90	6.285	3.96	7.251	2.292	3.16

*Percentages based on oven dry weight of ash used.

In both tops and roots the percentage of calcium oxide is greater than the percentage of magnesium oxide in every case. This is to be expected, since such a relationship holds in general for all plants. The presence of caliche near the surface apparently does not affect the absorption of calcium by Larrea, since the tops of plants growing on areas TB and LI, where caliche was either absent or more than four feet below the surface, contained respectively both the lowest and the highest percentage found. Although the chemical analysis of soil from LI showed no calcium present in the first eight inches, the soil at greater depths must contain as much as the other areas, since the tops of plants from this area yielded the highest percentage of calcium oxide.

Differences existing between the plants from the different areas in respect to the percentages of calcium oxide and magnesium oxide which they contain or the calcium-magnesium ratios do not correlate with differences in the range or with changes in the osmotic values of the sap of leaves and twigs from plants growing on the areas. The hydrogen ion concentrations of the soil solutions of the four soils from the selected areas as determined with the quinhydrone electrode were practically equal. The greatest difference in pH was 0.19, most of which difference could be accounted for as experimental error since considerable "creeping" of the potential occurred during the measurements. This "creeping" as reported by McGeorge (1929) was probably due to the presence of manganese in the soil.

DIURNAL CHANGES IN THE OSMOTIC VALUE AND MOISTURE CONTENT OF THE LEAVES AND SMALL TWIGS

The variations in moisture content and osmotic value of the leaves and twigs were quite regular throughout the 53 hour period during which the samples for this experiment were collected.[3] As will be seen from Figure 5 the maximum sap concentration for bush A came at 3 p.m. on both days while the maximum for bush B was found at 1 p.m. on both days. This lag on the part of bush A was probably due to two factors; first, bush

[3] The writer is indebted to Mr. E. H. Runyon for determinations of the moisture content.

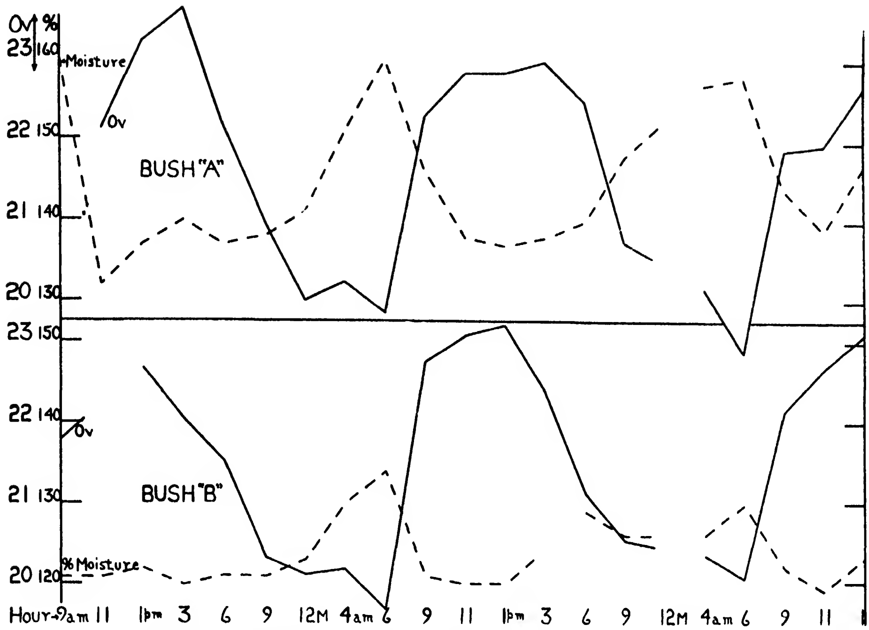

FIG. 5. Diurnal variations in osmotic value and moisture content of leaves and twigs of Larrea. Data for bush A above, for bush B below. Prolonged breaks in the graph lines indicate no determinations for those dates.

A was considerably larger than B and therefore had a larger and more extensive root system to absorb moisture and, second, and no doubt more important than the first, bush A was growing in a pocket of soil surrounded by large rocks which form a basin and therefore the moisture content of the soil in contact with the roots was probably much greater than that around the roots of B, which was situated on an open, well-drained slope. These contentions are supported by the fact that the moisture content increased considerably more in A than in B during the night. Herrick (1933) found that the osmotic and suction tension values of *Ambrosia trifida* also reached their maximums between 1 and 3 p.m. daily.

The lowest osmotic values for the two bushes were found in the 6 a.m. collections from both bushes on both days. The rapid increase in osmotic concentration in the 3- to 5-hour period beginning around 6 p.m. is largely due to rapid transpiration. However, the increase in the photosynthetic rate and subsequent accumulation of the products of photosynthesis no doubt serves to increase the concentration of the cell sap also. The decrease in osmotic value which begins about 3 p.m. for bush A and 1 p.m. for bush B was accompanied by an increase in moisture content. This indicates that the rate of transpiration is checked at those times and that the moisture content is of greater importance than the photosynthetic rate in determining the concentration of the plant sap. Bush A with a greater range of osmotic concen-

tration (3.7 atmospheres) also had the greater variation in its moisture content (28 per cent). The soil moisture at 15 centimeters was about 1 per cent higher at B than at A. However, this difference is not very significant since owing to the location of A among very large rocks it was difficult to obtain a representative soil sample even at that shallow depth.

These results show that the time of day is important when samples for cryoscopic determinations or moisture content are being collected. All of the samples for a comparative study should be collected at as nearly the same time of day as possible. The least change occurs during the period from 11 a.m. to 1 p.m. and from 4 a.m. to 6 a.m. Collections made between 6 and 9 a.m. may vary as much as 3.7 atmospheres due to difference in time of collection alone.

INDIVIDUAL DIFFERENCES IN OSMOTIC VALUE BETWEEN LARREA BUSHES IN THE SAME HABITAT

Near the peak of the arid foresummer, July 1st, ten samples of leaves and small twigs were collected on each area from ten different plants to determine how much difference in osmotic concentration existed between plants in the same habitat at a given time. The water deficit of the plants was so high at the time of collection that, as may be seen from Table 6, only a few of the samples from two of the areas yielded sufficient sap for a determination. Because of this failure to get enough juice from the tissues one-half of the experiment was repeated near the peak of the rainy season, August 8th, at which time all of the 8 samples collected on areas CB and CP yielded much more than the required quantity of sap. The values found for these samples, the average osmotic values, the differences between the highest and lowest osmotic values, and the greatest deviation from the mean osmotic value in each case are included in Table 6.

The results show that differences of over 8 atmospheres may exist in different bushes on the same area at a given time during periods of drought. During rainy periods, however, the differences tend to be somewhat less. In studies of this nature, as the above data indicate, it is better, where the size of the plant permits, to take the average of complete samples from individual plants when establishing the average osmotic value for a given species in a certain habitat rather than composite samples from a large number of individuals. And when one wishes to follow the changes in the osmotic value from time to time it is highly important that the samples be collected from the same bushes and in as nearly the same manner as possible each time.

GENERAL DISCUSSION

Of the conditions of the environment studied in this investigation soil moisture and rainfall apparently exert the strongest influence upon the variations in the osmotic value of the cell sap of the leaves and small twigs of

TABLE 6. Osmotic value differences between plants.

Sample	July 1st				August 8th	
	CB	CP	TB	LI	CB	CP
1	45.338	45.784	43.140	47.070	22.432	23.632
2	42.874	40.700	42.034	39.198	22.912	27.342
3	50.364	n. s. s.	42.202	43.728	24.568	24.040
4	n. s. s.	40.122	42.358	n. s. s.	23.500	26.094
5	46.746	n. s. s.	n. s. s.	n. s. s.	23.620	24.738
6	43.464	n. s. s.	34.910	n. s. s.	23.980	26.694
7	45.074	n. s. s.	n. s. s.	n. s. s.	22.144	28.340
8	n. s. s.	n. s. s.	41.672	42.166	21.724	27.990
9	43.692	n. s. s.	37.156	n. s. s.	......	......
10	47.166	41.758	36.038	n. s. s.	......	......
Average Ov.	45.590	42.091	39.951	43.040	23.110	26.045
Difference between highest and lowest osmotic values	7.490	5.662	8.230	7.872	2.844	4.708
Greatest deviation from the mean Ov.	4.774	3.693	5.041	4.030	1.458	2.413

*n. s. s. indicates that there was "not sufficient sap" obtained from the sample for a determination.

Larrea tridentata. This is to be expected, especially in a semi-arid region, and it is in accord with the findings of Korstian (1924) for plants in the Wasatch mountains of Utah. That he did not discount entirely the effectiveness of other factors is shown by the following statement: "The concentration of the sap of a species is not constant. It may be influenced by any of the environmental conditions affecting transpiration, the products of photosynthesis, or the supply of available soil moisture. Osmotic pressure in plants is more rapidly changed by fluctuations in the moisture conditions of the site than by temperature or light."

Differences in light intensity, temperature, and wind movement were not taken into account in this work since it is believed that they are very slight for the creosote areas studied. Spalding (1904) has shown that the transpiration rate of Larrea is governed by the supply of available moisture in the soil; the more water present, the higher the rate of transpiration.

That light is an important factor influencing the osmotic pressure of plant saps has been shown by several workers. Dixon (1910) noted that illumination increased the osmotic value in leaves while darkness decreased it. This he attributed to increases in the soluble carbohydrates in light. Chandler (1913) found that shading plants such as corn and Canada field peas 24 hours caused a decrease in the sap densities. In a study of the osmotic values of the cell sap of the leaves of certain evergreen trees Gail (1926) attributed fluctuations in the values during February and March to the effect of cloudy

days alternating with days of sunshine. Continuous cloudy weather caused a lowering of the osmotic pressure, owing to a decrease in the photosynthetic rate. These observations suggest that variations in light intensity and the accompanying variations in the rate of photosynthesis may be responsible for the fact that the osmotic value of the expressed sap of leaves and twigs of Larrea did not respond as quickly or as greatly at all times to a given change in the moisture content of the soil. A hard rain of short duration preceded and followed by periods of considerable sunshine might not affect as great a change in the osmotic values as would follow if the precipitation occurred during an extended period of rather cloudy weather, since the products of photosynthesis would then continue to be formed at the same rate and thus prevent the osmotic values from falling.

Returning again to a consideration of the influence of soil moisture content upon the osmotic value of the cell sap it may be pointed out that Iljin, Nazarova, and Ostrovskaja (1915, 1916) and others have reported a close correlation between increases in the osmotic pressure of plant cells and diminution in the water-supplying power of the environment. Hawkins, Matlock, and Hobart (1933) observed that the osmotic pressure and specific conductivity of the leaf sap of the Acala variety of cotton were usually inversely correlated with the available moisture supply. At certain times, however, they found that other factors modifying the transpiration rate affected these plant properties more than did the soil moisture conditions.

In general, the higher the moisture content of the soil the lower the osmotic pressure of the roots. The osmotic pressure of the leaves was frequently found to be higher than that of the roots and not always correlated with the latter although it too was markedly influenced by conditions of humidity. McCool and Millar (1917) observed that the moisture content of soils is closely correlated with the depressions of the freezing point of sap from corn, peas, and clover roots. The tops, however, were far less sensitive to variations in the soil moisture content. It is probable that if it were possible to make periodic determinations of the osmotic values of the cell sap of the roots of Larrea, as was done with the leaves, an even closer correlation would be found between the variations in soil moisture and the concentrations of the sap. Since all of the environmental conditions, except moisture content, are much less variable for the roots than for the aerial portions of the plant, it is to be expected that the former will respond more quickly and to a greater degree to variations in the available soil moisture.

That there is no set rate of change in response to changes in the environmental conditions seems evident from the data obtained during this investigation. The factors which determine the rate of change do not reside primarily inside the plant but are external to it. Differences such as existed between any of the areas studied were not of sufficient magnitude to produce perma-

nent changes within the plants which would alter their response to variations in the environmental conditions as measured by determinations of their osmotic values from time to time. Any difference in rate of change in cell sap concentration as between plants on different areas could always be attributed to some condition, usually soil moisture content, external to the plant. It would be very difficult to find two creosote bushes which would not respond similarly to all influences of the evironment if it were possible to transplant them into identical situations. In other words, there is nothing in this study to indicate that Larrea grows in habitats which are sufficiently different to require or produce fundamental and permanent variations in its internal adjustments—, variations, for example, which would cause the plant to respond more rapidly or less rapidly than a sister plant to a given range of environmental factors.

That it is possible temporarily to produce such plants experimentally is well known. Magistad and Truog (1925) were able to lower the freezing point of sap from corn plants as much as two degrees centigrade by applying fertilizer to the hill. This amount of change in the sap concentration was found sufficient to protect young corn seedlings in most cases from late spring frosts. The addition of mineral nutrients to soils, McCool and Weldon (1928) found, generally resulted in increased concentration of the same elements in the cell sap and consequently an increase in the osmotic value of the cell sap. Plants which have undergone a hardening process by exposure to gradually increasing lower temperatures are able to withstand sudden extreme drops in temperature much more successfully than plants which have not become "hardened." These changes, however, are quite temporary.

The rapidity with which all of the creosote bushes studied approach approximately the same osmotic values, as extreme conditions are approached, indicates that all plants of Larrea possess a fairly definite range of osmotic value variation. It is possible that had conditions of drought been more severe greater difference in the range of osmotic values for the respective areas would have been found. It is doubtful, however, whether the moisture content of the soil ever gets appreciably lower than it did in the habitats under consideration during the period of this investigation. It is possible, as has already been pointed out, that determinations of the concentration of the root sap might have proven to be a much better measure of the effectiveness of environmental differences on the various areas. Meyer (1929) has shown that unless the differences between two or more habitats is very great, the osmotic value of the expressed sap is not a dependable indicator of the type of environment.

In speaking of the investigation of the peculiarities of habits and physiological activities, Spalding (1904) wrote, "It is certain that a fairly intimate knowledge of even a limited number of desert species brings the conviction

that no general statement is an adequate expression of the biological relations of any one of them, that each is a law to itself, and that its actual relations to the environment must be determined for each species by critical study of its own structural and physiological characteristics, one by one."

The writer hopes that the results of this investigation will prove to be at least stepping stones toward a more complete knowledge of the relations of the creosote bush, *Larrea tridentata*, to its environment.

SUMMARY AND CONCLUSIONS

The purpose of the work reported in this paper was to determine the range and differences in the rate of change of osmotic values occurring in *Larrea tridentata*, a non-succulent, perennial, desert shrub, under natural conditions of growth, and to attempt to correlate these variations in range and rate of change with conditions of the environment. Although considerably more experimental work is necessary fully to accomplish this purpose, the following conclusions may be drawn from the data presented:

1. The maximum responses to the extreme changes in the environment are reflected in the osmotic values of the leaves of all creosote bushes in approximately the same length of time regardless of differences in the environmental conditions affecting the bushes during the period between the extremes. The rate of change in osmotic value is regulated by external and not by internal factors.

2. At the end of the rainy season the osmotic values of the leaf sap of creosote bushes in the region studied approach the minimum values and are practically equal in the different areas although rather wide differences may occur at intervals previous to this time. The same relationship holds with respect to the maximum osmotic values at the close of the arid seasons.

3. There are greater differences in the osmotic values of different creosote bushes during periods of drought when the maximum values are approached than during rainy seasons when changes in the osmotic pressures are in the direction of the minimum values. This may bè attributed to the possibility that the reactions of a plant are more greatly influenced by individual differences as the dessication of the tissues progresses.

4. Specimens of *Larrea tridentata* from different habitats display ranges of osmotic values for the leaf saps which are relatively specific for each habitat.

5. The greater the range of osmotic value for a given creosote plant or habitat the more successful and uniform the growth of Larrea.

6. Conditions of the environment other than rainfall or soil moisture content exert a strong influence on the osmotic value of the cell sap of leaves of Larrea, especially as the lowest and highest values are approached.

7. Layers of caliche near the surface are beneficial to those creosote

bushes the roots of which are able to penetrate the caliche, thus drawing upon the moisture stored beneath this layer.

8. Larrea bushes in different habitats exhibit approximately the same "osmotic inertia."

9. Variations in the total soluble salt content of the soil at 15 centimeters show from time to time, no correlation with the variations in the osmotic values of the leaves and small twigs of Larrea collected on the same dates.

10. The higher the total soluble salt content at 15 centimeters, within the limits of concentration found for the areas studied, the more successful the growth of the creosote bush.

11. The presence of "caliche" in close proximity to the root system does not effect the absorption of calcium by *Larrea tridentata.*

12. There is no correlation between the percentages of CaO and MgO contained in creosote plants, or the Ca/Mg ratios, and the range of osmotic values, or changes in the osmotic values, of the sap of leaves and small twigs of Larrea.

13. Collections of plant material for comparative sap concentration studies should all be made at as nearly the same time of day as possible because of the relatively large variations which occur throughout each 24-hour period.

14. During extreme conditions, differences in osmotic values of as much as 8 atmospheres may exist in the sap of different Larrea bushes in the same habitat.

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THE EFFECTS OF BLACK LOCUST ON ASSOCIATED SPECIES WITH SPECIAL REFERENCE TO FOREST TREES[1]

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Contents

THE EFFECTS OF BLACK LOCUST ON ASSOCIATED SPECIES WITH SPECIAL REFERENCE TO FOREST TREES

INTRODUCTION

For a number of centuries, it has been known among agriculturists that such crop plants as beans, peas, and clover lead to increased yields of certain other crop plants following in the rotation; but it remained for modern investigators to demonstrate that nodule formation on roots of leguminous species is due to infection by nitrogen-fixing bacteria and that through the activity of these bacteria the nitrogen content of the soil is increased. Beijerinck (1888) isolated and cultured the organism and named it *Bacillus radicicola;* Prazmowski (1889) changed the name to *Bacterium radicicola;* and later the Society of American Bacteriologists placed *Bacterium radicicola* in the genus, *Rhizobium,* that commonly in use at present.[2] Fred, Baldwin, and McCoy (1932) have assigned all leguminous species, whose nodule bacteria have been studied, to sixteen groups on the basis of interinoculations; thus, each species within a group may successfully be inoculated with bacteria from the nodules of any other species within the category. The bacteria inoculating roots of species in any one group are deemed distinct enough from those inoculating other groups to be considered as a separate species. Black locust (*Robinia pseudoacacia* L.) alone comprises "Group XII."

The exact process involved in nitrogen fixation by nodule bacteria is not yet understood. Maze (1898) believed that the slimy sheath of the organism, a product of sugar decomposition, combined with the atmospheric nitrogen resulting in the nitrogenous compound absorbed by plants. Spratt (1919) states, "The production of slime is connected with the amount of nitrogen fixed, and is influenced by the medium in which the bacteria are living." Blom (1931) investigated the three possible chemical processes by which nitrogen may be fixed in the organisms, oxidation, reduction, and direct union of nitrogen with some organic compound, and concluded that the fixation occurs through a reduction process. All of his evidence in support of this theory is indirect. According to Fred, Baldwin, and McCoy, "the process of nitrogen fixation begins as soon as, or shortly after, the formation of the nodules and continues as long as the nodules remain firm and healthy, and the plant is actively growing." Numerous authors investigating nitrogen fixation have concluded that after the fixation processes are completed the nitrogen does not become available to green plants until after the death and decomposition of the nitrogen fixing bacteria.

Although foresters have reported, during the last decade, their recognition of the importance of black locust as a benefactor to associated tree species, their data represent studies on comparatively few plantations with

[2] *Pseudomonas radicicola* is another name occasionally used.

associated species, primarily catalpa. Ferguson (1922), from studies of adjacent black locust and catalpa plantings at College Farm, State College, Pennsylvania, showed small but consistent decreases in total nitrogen content of the soil at increasing distances from the locust planting. Averages of three nitrogen determinations on soil samples taken in the black locust planting, in the adjacent tall catalpa, and in the catalpa farthest from the locust were, respectively, 0.102, 0.098, and 0.089 per cent. Ranges of average height and diameter[3] measurements of trees in nine successive rows away from the locust were 26.8 to 5.0 feet and 3.3 to 0.7 inches, respectively.

McIntyre and Jeffries (1932), since the collection of data in the present paper, also, have reported recent studies of soil nitrogen in relation to height and diameter growth on two catalpa plantings adjacent to black locust at the Pennsylvania State College, State College, Pennsylvania. For the first plot, the average height for rows 1, 2, 4, 6, 8, and 9 from the black locust planting ranged from 25.8 to 11.4 feet and the average diameter from 4.20 to 1.91 inches; and for rows 1, 2, 4, 6, and 8 of the second plot from 25.1 to 14.0 feet and 3.46 to 2.53 inches, respectively. Both total and nitrate nitrogen analyses were made on soil samples from each plot. The percents of total nitrogen in the first plot found from samples taken in the locust grove, between the first and third rows of catalpa from the locust grove, and between the seventh and ninth rows of catalpa were 0.1463, 0.1316, and 0.1263. The amounts of nitrate nitrogen in the same samples were, respectively, 8.2, 8.9, and 1.8 parts per million of air dry soil before incubation, and 75.3, 68.7, and 36.9 after incubation for thirty days at 22 to 25° C. with a moisture content of the growth media of about 22 per cent. Their check data from an adjacent oak woodlot have not been included. Results of studies on the second planting were quite as indicative of the effects of locust on height and diameter growth of catalpa and nitrogen content of soil as those of the first planting.

Black locust may become established under varying combinations of site factors. Cuno (1930) suggests that the range of black locust may have been originally restricted to the Appalachian Mountains from Pennsylvania to Georgia and to parts of western central Arkansas and eastern central Oklahoma. He further states that the best development of the species occurs on the western slopes of the Appalachians in West Virginia. This tree has been introduced into practically every state for one or another of its many uses. In the western states, eminent success with plantations has been attained in the valleys of the northern Rocky Mountain region, particularly, in Idaho, eastern Oregon and Washington. Black locust was introduced into Europe in 1601 and has been considered the most successful of tree species introduced from America. Although establishment of locust is often found on badly eroded, rocky slopes, the high rates of growth usually occur only in planted or natural stands on well drained silty loams.

The writer found from observations throughout the states of Ohio and

[3] Tree diameters are measured at a height of four and one-half feet from the ground.

Indiana, during the summers of 1931 and 1932, that the black locust-catalpa combination is the usual one from which comparative measurements may be obtained. Suitable plantations were also found, however, when data on the relation of locust to the growth of white ash, tulip poplar, black and chestnut oaks were collected.

The purpose of the present investigation was to obtain more critical data to demonstrate to what extent black locust affects the soil nitrogen content and the growth rate of associated species. Studies have been confined to plantings of species adjacent to locust in the states of Ohio and Indiana and recently established plots in the Botanic Garden at The Ohio State University.

The writer wishes to express appreciation to Dr. E. N. Transeau and Dr. H. C. Sampson of the Department of Botany, The Ohio State University, and to members of the Central States Forest Experiment Station staff, collaborating in the study, for helpful suggestions and criticism during the progress of the investigation.

PLANTATIONS

Six plantings have been included in the major part of this investigation; one in Highland County, Ohio; one in Clermont County, Ohio; and four in Clark County, Indiana. Several other plantings in various counties of Ohio have been supplemented for less detailed study. All of these have been established twenty years or more.

Methods. Rectangular plots were laid out in representative parts of the plantations adjoining the black locust. In every case, the trees were spaced at regular intervals in rows paralleling those of the locust, and the widths of the plots were sufficient to include from 6 to 20 trees in each row. By using a Forest Service hypsometer and a diameter tape, the height and diameter of each tree on the plots were obtained. Later, the mean height and diameter were calculated for each row.

In the collection of the soil samples at regular intervals of distance from the locust, care was exercised to remove the litter and duff to the mineral soil. Each sample, a composite of four to six samples well distributed across the plot, was taken from the upper 6 inches of the profile, placed in cardboard containers, and immediately treated with a few drops of toluol to stop bacterial action. Within a few hours all samples were thoroughly air dried by spreading out on sheets of paper. Previous to the analytical work, the soil was pulverized and sieved through a 10-mesh screen.

Total nitrogen determinations were made in duplicate on 10-gram soil samples from each collection by the boric acid modification of the Kjeldahl method.

Hydrogen-ion concentrations for the several soil samples were obtained by means of a quinhydrone potentiometer. Ten-gram quantities were each well agitated in 100 cc. of distilled water, the bottles stoppered, and allowed

to stand for twenty-four hours before making the determinations (Ref. in Bailey).

Increment borings[4] were taken from trees near to and at a distance from the locust in six Ohio catalpa plantings. From the cores, a comparison was made of the growth rate for the first 10-year and the last 10-year periods of the two groups.

During the summer of 1931, observations were made on relative degrees of nodulation on grazed and ungrazed locust plantings and also in plantings on various soil types.

Results and Discussion. The greater portion of the results from the study of the plantations are presented in eight figures and three tables. Figure 1

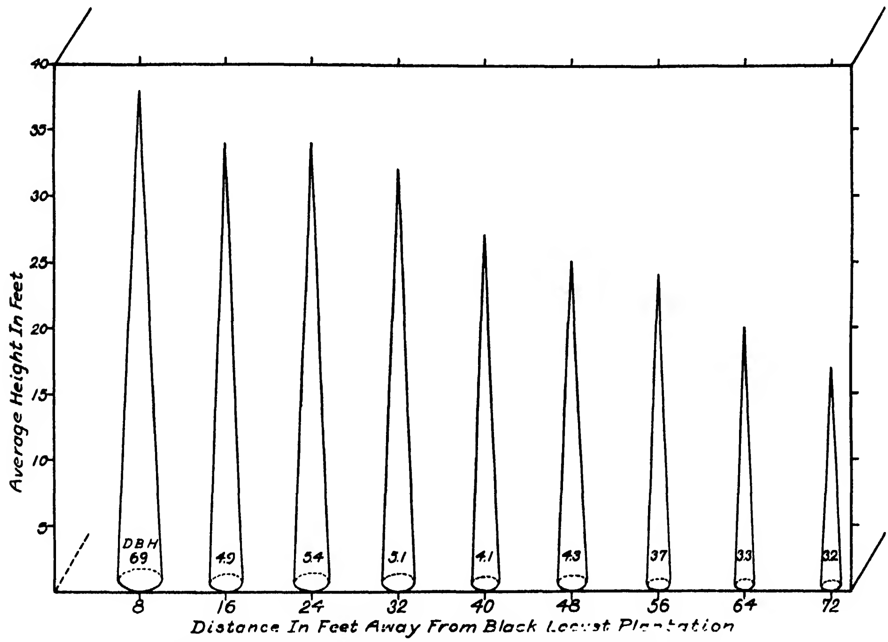

Fig. 1. Average heights and diameters for twelve catalpa trees in each of nine rows at increasing distance from black locust in plot 3.

contains average height and diameter data collected on plot 1 in the catalpa (*Catalpa speciosa,* Warder) planting situated between two black locust plantings in Clermont County. Figure 2 clearly shows the V-shaped dip in the canopy of the catalpa, the shortest stems growing midway between the locust plantings. The arrow designates the first row of black locust on the right; the first row on the left is just beyond the limit of the figure. Annual ring counts showed each species to be 21 years old. The area is generally level with slight surface drainage to the east. As no grazing has occurred since

[4] Increment borings, showing annual rings from the pith to the cortex, were taken at 8 inches from the ground.

FIG. 2. Cross-section of catalpa planting, containing plot 3, situated between two black locust plantings; arrow designating first row of locust on right; locust on left just outside margin of figure.

TABLE 1. Average heights and diameters for trees in rows at increasing distance from black locust in plots 2, 3, 4, 5, 6, and 7.

Plot-2 (Catalpa)			Plot-3 (Catalpa)			Plot-4 (White Ash)			Plot-5 Tulip poplar Black oak			Plot-6 (White ash)			Plot-7 Tulip poplar Black oak Chestnut oak		
Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.	Distance from black locust	Average height	Average D. B. H.
Feet	*Feet*	*Ins.*	*Feet*	*Feet*	*Ins.*	*Feet*	*Feet*	*Ins.*	*Feet*	*Feet*	*Ins.*	*Feet*	*Feet*	*Ins.*	*Feet*	*Feet*	*Ins.*
6	40	6.0	6	44	7.5	5	49.0	6.4	5	52.5	7.5	5	52.5	4.7	5	53.5	5.2
12	40	5.8	12	45	7.8	10	41.0	4.1	10	x	x	10	49.7	4.0	10	x	x
18	39	5.2	18	43	7.5	15	39.0	2.9	15	59.7	8.3	15	62.0	5.4	15	46.2	5.3
24	37	5.5	24	42	7.6	20	45.0	4.6	20	x	x	20	x	x	20	x	x
30	35	4.9	30	36	5.4	25	x	x	25	x	x	25	38.5	3.1	25	52.0	6.4
36	35	4.9	36	35	5.5	30	32.5	3.2	30	46.5	5.9	30	45.0	4.2	30	41.0	3.8
42	33	4.9	42	35	5.5	35	44.0	4.7	35	51.0	7.3	35	34.0	3.4	35	40.5	3.8
48	32	4.8	48	31	4.8	40	43.5	4.7	40	43.0	5.3	40	x	x	40	39.0	3.5
54	33	4.6	54	27	4.9	45	41.5	4.7	45	32.0	3.2	45	33.5	2.8	45	24.5	2.5
60	33	5.0	60	31	5.5	50	31.0	3.5	50	43.0	4.8	50	34.7	3.3	50	40.0	3.7
66	31	4.3	66	....	....	55	24.0	2.3	55	35.5	3.8	55	30.3	2.9	55	34.5	3.7
72	31	4.6	72	....	....	60	18.7	1.6	60	29.0	2.6	60	32.5	3.2	60	x	x
78	31	4.7	78	....	....	65	23.0	2.2	65	27.5	2.7	65	27.5	2.6	65	x	x
84	31	4.4	84	....	....	70	25.2	2.6	70	34.5	3.9	70	35.5	3.8	70	25.3	3.1
						75	29.6	3.3	75	32.0	2.5	75	27.0	2.7	75	x	x
						80	24.1	2.6	80	x	x	80	26.7	3.0	80	21.5	1.4
						85	25.5	3.0	85	34.0	3.0	85	24.0	2.5	85	25.0	2.7
						90	19.2	2.3	90	35.0	3.2	90	21.5	2.1	90	26.7	3.4
						95	26.5	2.8	95	34.7	3.1	95	25.0	2.8	95	26.0	3.0
						100	19.8	2.2	100	32.0	3.2	100	24.0	2.5	100	24.0	3.3
						105	19.6	2.6	105	33.8	3.2	105	20.0	2.1	105	23.0	2.5

the plantings were made, the Clermont silt loam is well aerated in the upper horizons. Decomposing litter has resulted in accumulation of humus from one-eighth to one-fourth inch in thickness. The greater portion of this humus formed beneath the locust.

Table 1 shows the mean heights and diameters for successive rows of catalpa in Highland County plots 2 and 3, established, respectively, on the west and east sides of the intervening black locust plantation. Figure 3 includes a part of plot 3 which shows the taller locust grove at the left and the catalpa on the right; the arrow marks the first row of catalpa. A very notice-

FIG. 3. Cross-section of plot 2, locust planting on left and catalpa on right; arrow pointing to first row of catalpa.

able decrease in the height of the catalpa is evident with increasing distance from the locust. From increment borings, the age of each species was found to be 25 years. The stand is growing on Clermont silty clay loam which has been slightly compacted by occasional grazing. A very gentle slope drains the area to the northeast.

Table 1 also contains mean height and diameter measurements on the Clark County plots 4, 5, 6, and 7. Plots 4 and 6 were located in pure stands of white ash (*Fraxinus americana* L.), plot 5 in mixed stand of tulip poplar (*Liriodendron tulipifera* L.) and black oak (*Quercus velutina* Lam.), and plot 7 in a mixed stand of tulip poplar, black oak, and chestnut oak (*Quercus montana* Willd.) These stands are 25 year old plantings situated on either side of two locust plantings of the same age. A gentle slope drains the area to the southeast. The soil, Rossmoyne silt loam, is well aerated in the upper part of the profile.

Although there are numerous minor irregularities in the trend of mean tree heights and diameters (Table 1, plots 4 to 7), Figures 1, 2, and 3 and Table 1 distinctly indicate for each plot a decrease in the dimensions of all species as the distance from the locust plantings increases. Recognizing that situations upon which investigations of this nature may be made are infrequent, the writer was careful to select for study those in which differences in topography, soil type, degree of pasturing, and age of locust and adjacent species played no significant rôle. It may be noted that for the Clark County plots data are lacking for a few of the rows. In these instances, there were too many overtopped trees to obtain representative average heights and diameters.

Figure 4 gives the results of total nitrogen analyses on the series of soil

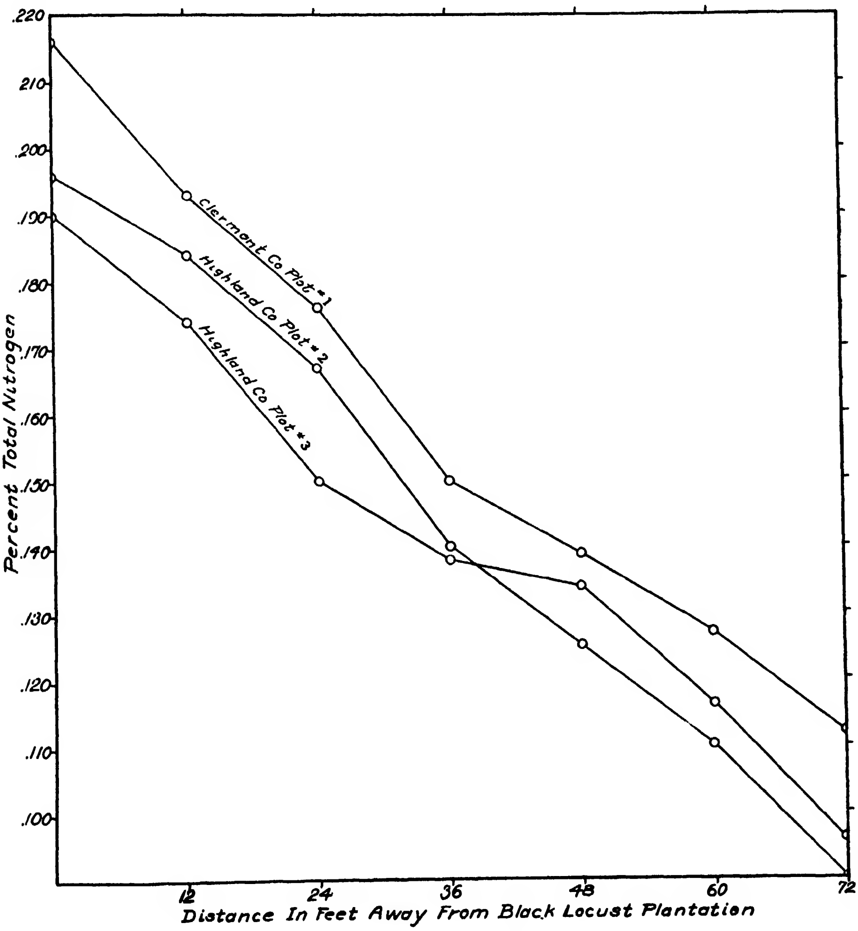

FIG. 4. Percentage of total nitrogen based on 10-gram air dry soil samples from plots 1, 2, and 3.

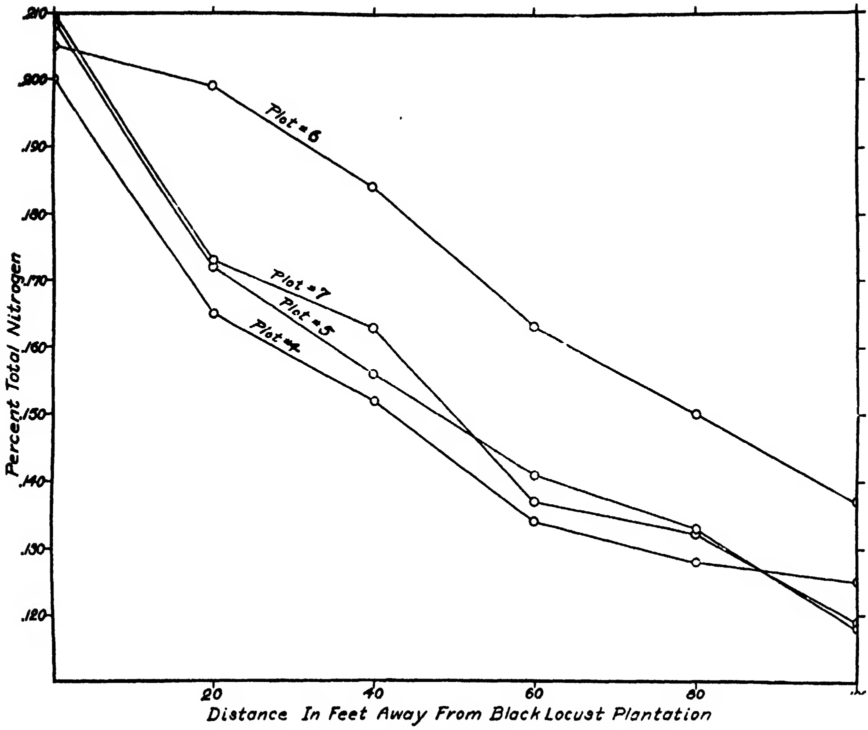

FIG. 5. Percentage of total nitrogen based on 10-gram air dry soil samples from plots 4, 5, 6, and 7.

samples from plots 1, 2, and 3. Figure 5 shows similar data for plots 4, 5, 6, and 7. The figures clearly indicate the rapid decrease in the per cent of total nitrogen content of soil, with increasing distance from the locust. The decrease is somewhat more striking in the plots on Clermont silt loam, a soil type generally very low in organic matter. A range from 0.09 per cent to 0.195 per cent total nitrogen may appear to be small; but, quantitatively, it is equivalent to a range from 1800 pounds to 3900 pounds of nitrogen per acre when based upon two million pounds weight of the top 6 acre-inches of soil. These observed variations in the nitrogen content of the soil and the height and diameter variations of the several tree species on the various plots present a significant correlation.

While the response of the subordinate vegetation to the presence of black locust was of minor importance in the study, Figures 6 and 7, showing orchard grass (*Dactylis glomerata* L.) under catalpa in plot 2, and under adjacent locust, illustrate one of many similar contrasts in growth rates of ground cover species observed by the writer. McIntyre and Jeffries, Cope, and others have reported numerous similar observations. The two exposures (Figs. 6 and 7) were obtained from one set-up at the juncture of the catalpa

FIG. 6. Ground cover of orchard grass west from border of locust in catalpa, plot 1.

FIG. 7. Ground cover of orchard grass east from same position as in Figure 6 but under locust.

and black locust plantings by rotating the camera 180 degrees. On inspection of the two figures, the best measure of differences in the quantity of grass is the depth to which the lower portions of the tree trunks are hidden. The grass becomes sparser under the catalpa as distance from the locust increases. The difference in light intensity under the two species, due to the thinner foliage of the locust than that of the catalpa, is not thought to be a limiting factor here for the growth of orchard grass since the grass development was only slightly better beneath large openings in the catalpa canopy than elsewhere beneath the same species.

The distance to which black locust affects the growth of other species has been little mentioned by investigators. Ferguson states, "Growing among the catalpa trees for a distance of forty feet are black locust trees started as seedlings and as root suckers." It is well understood that these distances will vary directly with the age of the trees and are further modified by such factors as soil aeration, soil moisture, and available essential mineral elements. In Figure 8 are indicated the locations of root suckers in plots 4 and 6 to afford some conception of the root spread of locust in the upper soil horizons. The number of suckers consistently decreases to zero at about 83 feet in plot 6. The gradation is not so characteristic of plot 4. No seedlings could be found on either of the plots. As black locust is quite intolerant to low light intensities, seedlings probably have been oppressed to starvation in the early stages of growth. Root suckers have been able to survive on translocated foods from the parent locust.

Other indications of differences in growth rates of trees adjacent to and at a distance from black locust are given in Table 2. These data consist of measurements of radial increase in inches at stump height of catalpa trees in plot 3, plot 2, and in one planting each in Warren and Green counties. The last two plantings are growing, respectively, in Clermont silty clay loam and Miami silt loam. The highest initial growth rate occurred in the trees of plot 9 adjacent to the locust. It is shown by the mean increments for all plots that the radial increase for the first ten years for the trees near the locust is greater than that for the same period for those trees at a distance. This relationship holds also for the last 10-year period for the same trees. It is clear that the difference in average volume increases is much greater than the radial increases denote. If the spread between the averages of the radial increases for trees adjacent to and trees at a distance from the locust, for each plot, for the first 10-year period be compared with the corresponding spread for the last 10-year period, the latter is shown to be greater. These observations indicate that growth curves based on radial measurements in these plots would, in general, be diverging.

The degree of nodulation on the roots of black locust and hence the

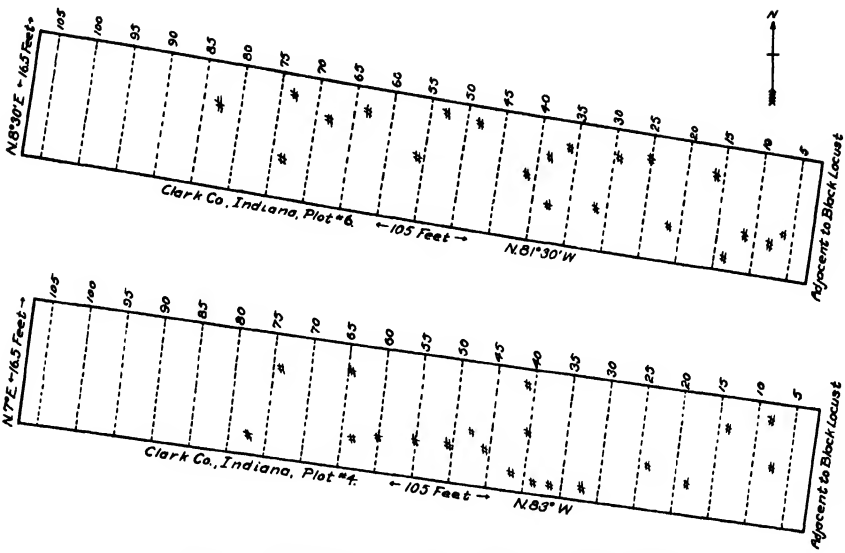

FIG. 8. Distribution of root suckers in plots 4 and 6.

amount of atmospheric nitrogen fixed vary with certain physical conditions in the soil. Examination of many roots in numerous plantings in Ohio and Indiana showed that minimum nodule formation occurred in those areas which were heavily grazed or water-logged for long periods in the year. In the grazed plantings, the few nodules present were small and occurred at the base of trees near the soil surface. Both the old and recently developed tubercles were small. In the water-logged plantings, the few nodules present were mainly in the upper one or two inches of soil, but were distributed much more widely than in the pastured areas. A characteristic common to both the heavily grazed and water-logged soil was poor aeration and, therefore, an insufficient amount of free oxygen for the aerobic nitrogen-fixing bacteria. Clearly, this was the limiting factor in nodulation in these plantings. Nobbe and Hiltner (1899) found that nodules on the roots of black locust, when submerged in water, are of little or no benefit to the host plant.

In the ungrazed plantings, nodulation was at its maximum in well drained, porous, silt loams over which had accumulated layers of humus and leaf litter. The position of most of the nodules in the soil profile was between the mineral soil and the humus or in the upper inch of the mineral soil. In such an environment, the moisture supply was adequate for nodule development even during the dry season of 1931. Where accumulation of humus and litter was scant and periodic drying of the surface soil occurred, the greatest abundance of tubercles was found somewhat deeper; but in no place were many nodules found below a depth of six inches. McIntyre and Jef-

TABLE 2. Radial growth of catalpa at stump height for both first and last ten-year periods, based on six successive trees in rows adjacent to and at different distances from locust.

Plot No.	Near Locust, Growth in Inches		Away from Locust, Growth in Inches		Location and age of plots
	First 10 Years	Last 10 Years	First 10 Years	Last 10 Years	
			72 feet from locust		
	1.80	1.50	1.40	0.75	On Delmar Jester farm,
	1.40	1.40	1.10	0.70	Clermont Co., Ohio.
3	1.95	1.25	1.70	0.60	Age 21 years.
	2.05	1.80	1.25	0.65	
	2.00	1.75	1.50	0.65	
	1.60	0.95	1.25	0.55	
Average......	1.80	1.44	1.36	0.65	
			60 feet from locust		
	1.85	2.15	1.60	1.25	On Edward Raousch Farm,
	2.30	2.10	1.20	0.55	Highland Co., Ohio.
2	2.10	1.75	1.10	0.80	Age 24 years.
	2.00	2.00	1.35	0.90	
	2.20	1.60	0.90	0.40	
	2.15	1.60	1.65	0.80	
Average......	2.10	1.86	1.30	0.78	
			60 feet from locust		
	2.10	1.25	1.25	0.70	On Henry Giehl farm,
	1.70	1.10	1.65	1.10	Warren Co., Ohio.
8	2.05	1.70	1.55	1.20	Age 20 years.
	1.70	1.35	1.65	2.10	
	1.50	2.50	1.40	1.35	
	2.00	1.65	1.90	0.95	
Average......	1.84	1.59	1.56	1.23	
			80 feet from locust		
	3.40	1.40	1.75	0.50	On Theodore and Max
	2.70	1.60	1.95	0.80	Zink farm, Greene Co., Ohio.
9	2.80	1.35	2.40	0.95	Age 24 years.
	1.65	1.50	2.05	0.70	
	2.60	1.30	1.85	0.60	
	2.85	1.40	1.85	0.80	
Average......	2.66	1.42	1.97	0.72	

fries quote Beijerinck (1918) as observing that black locust has few and small nodules. This observation is true for only certain combinations of site factors. The writer has frequently observed nodules in great abundance, a few having dimensions exceeding 0.5 by 0.2 inches.

There is little discrimination to be made on the relative amounts of nodulation by black locust in soil types whose parent materials are of different geological origin, provided such factors as soil moisture, soil aeration, and

organic matter content of soil are approximately equivalent. No definite range of pH tolerance can be cited for the locust bacteria, but it is known to be wider than for the bacteria of some of the field crop legumes. Cope states that the bacteria of black locust are more acid tolerant than those of alfalfa. By growing soy beans under three sets of conditions, "first, by varying the amount of calcium and inversely the degree of acidity; second, by varying only the acidity at constant amounts of calcium; and third, by varying only the calcium at constant acidity," Albrecht (1932) found that increased nodulation accompanied increased available calcium in the "growth media" but did not accompany or follow increased pH. This suggests that a correlation between a pH range and the amount of nodulation for black locust would be of questionable significance. Table 3 represents soil reaction and total nitrogen determinations made on soil samples collected from black locust and adjoining plantations growing on different soil types. It may be noted

TABLE 3. Soil reaction and percentage of total nitrogen of soil samples from locust and adjacent plantings on different soil types in Ohio and Indiana.

Plot location	Soil type	pH		Percentage of total nitrogen	
		Under locust	Under other species	Under locust	Under other species
Clark Co., Indiana					
Plot-4	Rossmoyne silt loam	6.72	7.02	0.200	0.125
Plot-5	Rossmoyne silt loam	6.88	6.45	0.208	0.118
Plot-6	Rossmoyne silt loam	6.79	6.97	0.205	0.137
Plot-7	Rossmoyne silt loam	6.49	6.68	0.209	0.119
Clermont Co., Ohio Plot-3	Clermont silt loam	6.46	6.15	0.216	0.112
Highland Co., Ohio Plot-2	Clermont silty clay loam	5.36	5.52	0.192	0.096
Greene Co., Ohio Plot-9 (Catalpa)	Miami silt loam	6.44	6.88	0.211	0.182
Morrow Co., Ohio Plot-10 (Catalpa)	Volusia silt loam	5.33	5.77	0.253	0.194
Morrow Co., Ohio Plot-11 (Catalpa)	Immature soil. Parent material sandstone and shale	4.44	5.16	0.345	0.139
Delaware Co., Ohio Plot-12 (Catalpa)	Miami silty clay loam	5.36	5.28	0.246	0.160

that the pH range in the locust stands is from 4.44 in the immature soil of Morrow County to 6.88 in plot 5. While nodulation was good in all of these plantings, the maximum development of tubercles was beneath a thick humus and in the upper two inches of the immature acid soil in plot 11. There is no indication that the acidity range found in these areas has set any limitations on nodule formation. Hall (1932) found no correlation between soil reaction and degree of nodulation in more than two hundred widely distributed black locust plots.

According to McIntyre and Jeffries, "Black locust does well on the so-called acid soils of Pennsylvania such as DeKalb, Berks, and Volusia, and the authors believe that factors other than soil acidity, particularly the presence of the particular group of bacteria associated with this species, are of more importance." Cope states that special inoculation material is used in New York in many instances to inoculate soil for seeding black locust. During the summer of 1932, the writer examined more than one hundred locust plantings and as many stands of natural reproduction in Ohio, Indiana, and Michigan but failed to find one without enough tubercles present to indicate that inoculation had not occurred. Also, an attempt by the writer to grow locust seedlings in framed plots in the Botanic Garden without root infection by nodule forming bacteria failed, even though the soil had been treated to a depth of one foot with a three per cent solution of formalin one week before seedlings from sterilized soil were planted. Many flats of locust seedlings, growing in the greenhouse in soil media which had been autoclaved at fifteen pounds pressure for four hours, became inoculated with no special attention being given to prevent or effect bacterial transfer. From these experiences, it seems that the bacteria are of such common occurrence that failure of locust to become inoculated is unlikely.

Garden Plots

As preliminary work in the field had clearly demonstrated that black locust is effective in increasing the growth rate of certain associated species, the garden plot study was begun to determine how soon the effects would be perceptible.

Methods. Soil, underlain by limestone glacial outwash gravel, was excavated to a depth of 12 inches along a terrace contour for eleven plots 4 feet square and 2 feet apart. Frames constructed from boards 1 inch thick by 14 inches wide were fitted into the excavations so that about 2 inches projected above the ground level. The excavated soil material was returned to the frames by passing through a sieve with one-quarter inch meshes. Care was observed to give all the plots uniform horizontal surfaces.

The seedlings of black locust and Chinese elm (*Ulmus pumila* L.) used for planting were grown from seed[5] in the Department of Botany green-

[5] Seed was obtained from the Katzenstein Seed Company, Atlanta, Georgia.

house. Seeds of locust, dusted with Semesan[6] for disinfection, had been sown in small flats of sandy soil material which had been sterilized in an autoclave at 15 pounds pressure for 4 hours. The elm seed had been sown in similar flats that had not been sterilized.

The 6 weeks old stock was transplanted to the garden 6 inches apart in rows at the same intervals on June 1, 1931. Only elm was planted in plots 2, 4, 6, 8, and 11 while locust was alternated with the elm in the rows of the remaining six plots. Before setting each locust plant in place, its root system was dipped into an inoculum prepared from fresh tubercles.

In the dry periods of the growing seasons of 1931 and 1932, the plots were occasionally watered and well weeded. As the locust grew more rapidly than the elm, it was necessary frequently to clip those branches exceeding the height of the elm.

Well distributed soil samples were collected from the surface 4 inches in each plot on June 23, July 13, August 9, September 2, September 22, October 12, and November 10 in the second season. These were promptly air dried, sifted through a 10-mesh sieve, and placed in containers for future analysis.

Also, samples of elm leaves were gathered from each plot on the dates of soil collection. Each sample was composed of all ages of leaves from the entire elm population of the individual plots. The last collection was made when the leaves were turning brown and abscissing. The samples were dried at 80° C. to constant weight. They were then ground to a powder in a food pulverizer and stored in air-tight cans.

Total nitrogen was determined on 10-gram soil samples and 2-gram leaf samples by the boric acid modification of the Kjeldahl method, previously mentioned.

Results and Discussion. Figure 9 shows the fluctuations during the 1932 growing season in total nitrogen content of the soil for each of the pure elm plots. It is evident from inspection of the graphs that in general there was a decrease in the total nitrogen until a minimum was reached about September 2. Although there is an increase in nitrogen content in the plots after the low points, with ensuing decreases of the element in plots 4, 6, and 11, it is evident that on the dates of sampling subsequent to July 13 in no plot does the nitrogen present equal that of June 23. The conditions under which the plants of the various plots developed were deemed sufficiently similar to justify plotting an average of the amounts of nitrogen for each sampling date in order to present more clearly the general trend. These data are shown in the broken line curve.

It may be noted that the lower numbered plots had the higher initial percentages of total nitrogen. From the first plot through the seventh, there was a progressive decrement of organic matter in the soil; whereas for plots 7, 8, 9, 10, and 11 the organic matter was fairly constant.

[6] Semesan is a proprietary compound with active ingredient of hydroxymecurichlorophenol.

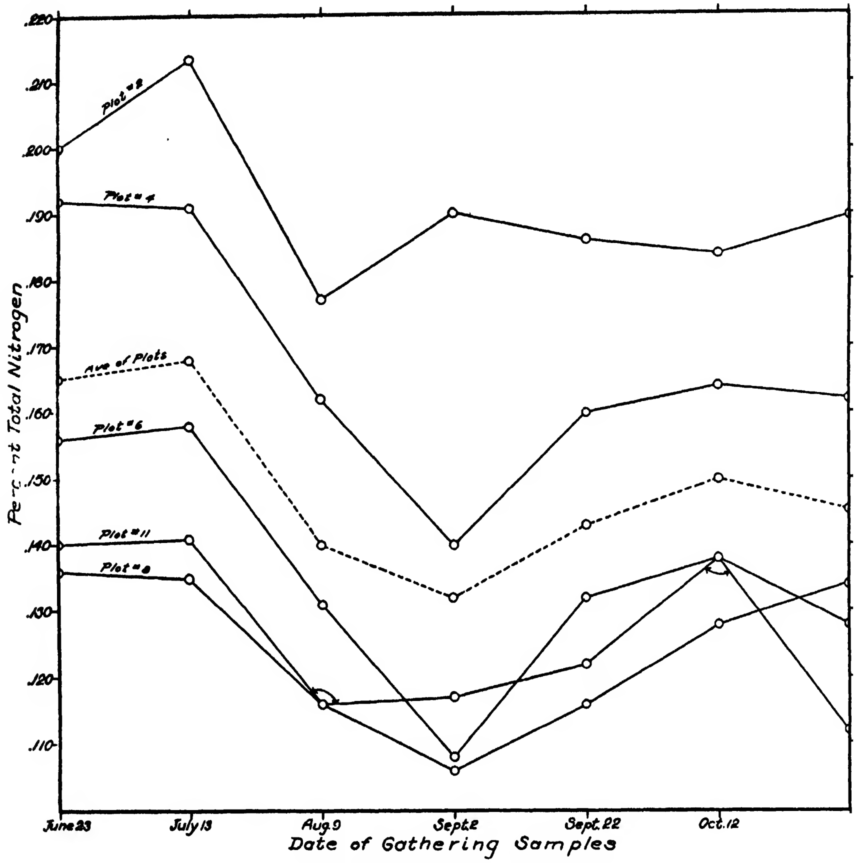

FIG. 9. Fluctuations of percentage of total nitrogen in soil of Botanic Garden elm plots for 1932 growing season.

In accounting for the drop in the total nitrogen content of the soil at the end of the summer, it should be known that the decline coincided with a severe drought for the terrace portion of the garden. As the underlying parent soil material of outwash gravel made underground drainage excessive, watering was not adequate to prevent recurrent soil desiccation to a depth of 3 to 5 inches. Any increases in total nitrogen should be attributed primarily to the non-symbiotic nitrogen-fixing bacteria. Decreases in total nitrogen indicate that absorption of soluble nitrogen compounds by the seedlings has been in excess of fixation of atmospheric nitrogen by the microorganisms.

The fluctuations during the 1932 growing season in total nitrogen content of the soil from the elm-locust plots are shown in Figure 10. The minimum content in general was reached about September 2 for the soil of the plots. During the period from September 2 to September 22, the nitrogen increment for these plots was much greater than for the elm plots. On November

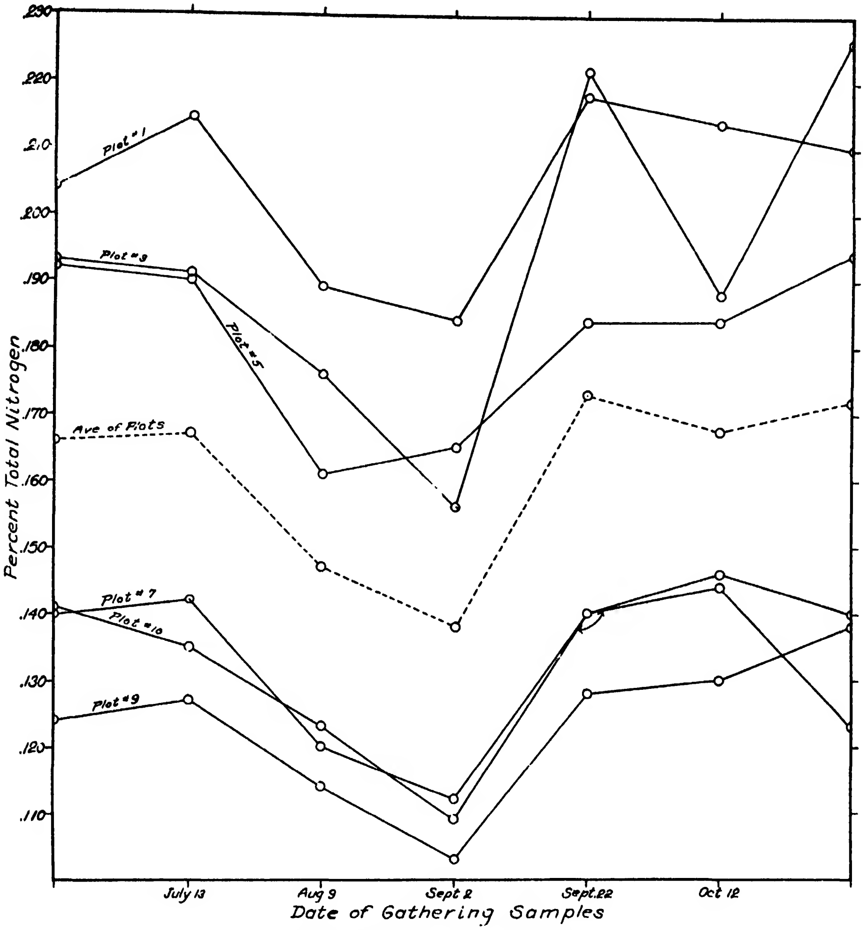

FIG. 10. Fluctuations of percentage of total nitrogen in soil of Botanic Garden elm-locust plots for 1932 growing season.

10, all plots except number 10 were found to have a nitrogen content equivalent to or greater than that on June 23.

As in Figure 9, the broken line curve represents averaged data from all of the plots. The average of analytical results for the initial soil samples is almost identical to the corresponding average of the elm plots, and the total nitrogen reduction on September 2 is less than that for the elm plots on the same date. The final average on November 10 shows a higher total nitrogen content than the corresponding value for the plots with no locust.

Alteration of nitrogen conditions by lateral leaching of soluble organic or inorganic substances or surface drainage into the plots was largely prevented by the sunken frames. The validity of the comparison cannot be discredited by differences in nitrogen absorption by the two species, as the more rapidly developing locust would absorb a greater quantity of nitrogen

than an equal number of less rapidly developing seedlings in the elm plots. In view of these data, it is inferred that the general increase of nitrogen of the elm-locust plots in excess of that of the elm plots is chiefly due to the presence of the black locust seedlings.

Examination of a few of the locust roots a month after transplanting the seedlings to the garden showed many small nodules present. The root systems were restricted to small areas the first year; but, during the second season, extensive fibrous roots with an abundance of large and small nodules developed in the upper 6 inches of soil.

In an effort to further detect any nitrogen changes in the soil material of the two groups of plots ascribable to the presence of locust, a series of

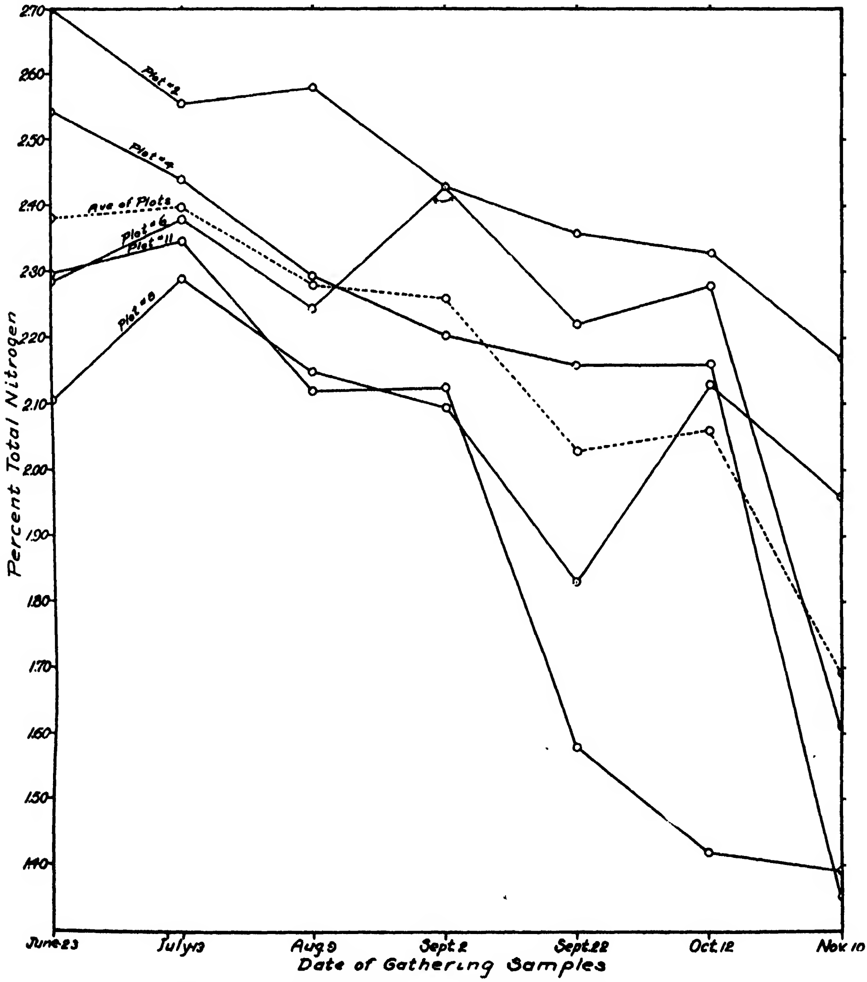

FIG. 11. Fluctuations of percentage of total nitrogen in oven dry elm leaves of Botanic Garden elm plots for 1932 growing season.

nitrogen analyses on the leaves of the associated elm was made. It is generally recognized that seedlings of different tree species behave differently under varying nitrogen conditions of the soil medium. The writer (1931) found that the total nitrogen content of the leaves of elm seedlings (*Ulmus americana* L.), produced under greenhouse conditions, were indicative of the varying quantities of total nitrogen in their soil media. For this reason, an elm species was planted with the locust for the present study.

Figure 11 shows the percentages, based on oven dry weight, of total nitrogen in the leaf samples obtained from the elm plots simultaneous with soil samplings. It is clear from the figure that, aside from the occasional increases in plot 6 and 8, there is a fairly consistent reduction in the leaf nitrogen content throughout the series. The broken line curve, representing average values, verifies this characteristic trend of the individual plot curves.

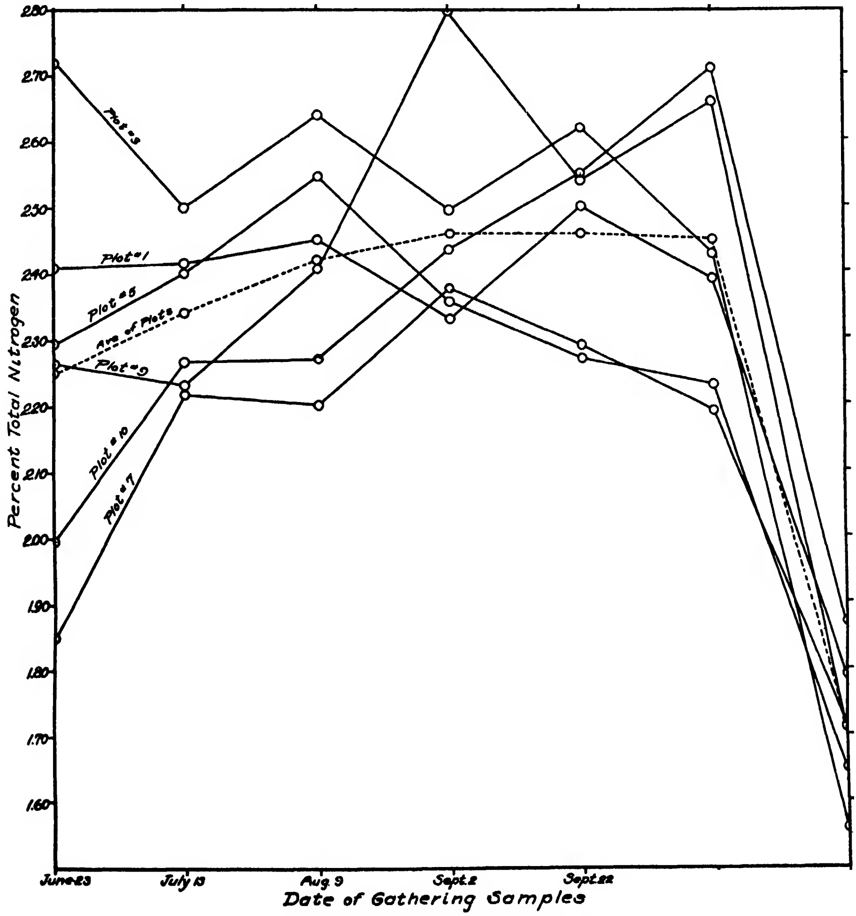

FIG. 12. Fluctuations of percentage of total nitrogen in oven dry elm leaves of Botanic Garden, elm-locust plots for 1932 growing season.

Results from nitrogen determination, corresponding in time to the above results but for the elm-locust plots, are shown in Figure 12. For the initial leaf samples, the nitrogen content is generally lower on the elm-locust plots than on the elm plots. This may be partially due to the greater exhaustion, during the spring, of available nitrogen in the soil by the more rapidly growing locust seedling. Since the overshadowing of elm was prevented by clipping off the upper locust branches, it is improbable that the differences in light intensities in the canopies of the pure and mixed plantings was sufficient to produce a difference in the carbohydrate-nitrogen ratios in the elm leaves of the two plantings.

The average plot curve shows; first, a gradual percentage increase of leaf nitrogen until September 2, in contrast to that of the elm plots; second, a constant nitrogen content until October 12; and, third, a sudden drop in total nitrogen on November 10.

The sharp decrease in leaf nitrogen content for nearly all of the plots (Figures 11 and 12) on November 10 is noteworthy. The percentages of nitrogen represented in the two figures for November 10 are based on yellow, abscissing leaves. Already existing soluble nitrogen compounds in the leaves, and the soluble forms resulting from processes of decomposition during the yellowing and hence the browning period, apparently move into the stems. However, some of the nitrogen loss to the leaves may be due to leaching by rain. Combes (1926) and others have found increases of nitrogen in stems following the yellowing period in autumn. Ebermayer (1888) and others have found the percentage of nitrogen in fallen leaves less than that in dried green leaves. This decrease of nitrogen content of leaves at the time of abscission then is a common phenomenon and is not peculiar to the conditions of this study.

Summary

1. An investigation has been made of the effects of black locust on soil nitrogen and on the growth rates of associated species in forest plantings in Ohio and Indiana. Studies of total nitrogen changes were also conducted during the 1932 growing season on the soil and leaves of elm seedlings of eleven garden plots containing elm in pure stand and in mixture with black locust.

2. In plantings of catalpa, white ash, tulip poplar and black oak, mixed tulip poplar, black oak, and chestnut oak adjacent to black locust, where such site factors as differences in topography, soil types, grazing, and age of locust and adjacent species were irrelevant, appreciable decreases in the heights and diameters of trees with increasing distance from the locust were found.

3. Analyses of soil samples, collected at regular intervals from the locust in each of six Ohio and Indiana plantations, indicated reductions in total

nitrogen as distance increased. These reductions in each plot showed definite correlations with reduction in mean heights and diameters for adjacent trees.

4. Definite decreases in the number and in the degree of development of ground cover species were observed as distance from the locust increased.

5. Increment borings have shown that the differences between the radial increases for the first and last 10-year periods for catalpa adjoining black locust was less than that for the same periods for catalpa at distances from the locust; and that the difference between the radial increases for the first 10-year period for adjacent catalpa and catalpa at distances from the locust was decidedly less than the difference between radial increases for the last 10-year period for the same trees.

6. Nodulation was at a maximum in the upper 4 inches of soil where a moderately constant moisture content, a high percentage of organic matter, and good aeration existed.

7. Although poor nodulation was found in many plantings and in naturally reproduced stands of black locust, evidence from field and garden plot studies indicates that, rather than absence of locust bacteria, poor aeration, poor moisture conditions, or both were the primary causes.

8. No correlation between soil reaction and degree of nodulation was evident from studies in locust plantations growing on different soil types.

9. Significant increases in amounts of total nitrogen were detected during the second growing season in the soil and leaves of elm of the elm-locust garden plots.

10. An appreciable decrease in the total nitrogen content of the soil of the elm plots was found at the end of the 1932 growing season.

11. During the summer of 1932, progressive decreases occurred in the total nitrogen content of the leaves of elm from the garden elm plots.

12. The results of this study provide additional data showing the effects of black locust on species associated with it. The details of the processes involved in the production of these effects have been aside from this study and should be the subject of further investigations.

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THE ORIGINAL FOREST TYPES OF SOUTHERN NEW ENGLAND[1]

By STANLEY W. BROMLEY

"The path led through woods which bore the mark of centuries, over barren hills that had been licked by the Indians' hounds of fire. . . ."

—*The Old Bay Path*, J. G. Holland.

[1] **Papers from Department of Botany, the Ohio State University, No. 336.**

Contents

THE ORIGINAL FOREST TYPES OF SOUTHERN NEW ENGLAND

Introduction

To reconstruct the appearance of southern New England[2] when the forest was the domain of the Indian, wolf, and rattlesnake is indeed an interesting but difficult problem after the nearly complete obliteration of natural features by more than two centuries of cultivation, grazing, and industrialization. It is the common assumption that most of the country was originally wooded—but what were the forest types, what was the character of the forest, and what were the influences to which it was subjected compared with those of the present day? Obviously, any idea of the original conditions may be gained only through a composite study of the ecology of the present day forest and the meager records of the past.

Inasmuch as the original woodlands were destroyed early in the settlement of the country, little light can be shed on the problem of original types by correlating soil or climatic factors with the present associations, composed as they are largely of secondary species or of secondary communities. The historical factors must therefore be given consideration in outlining the original forest types. The present paper deals largely with this phase.

A method of studying the historical factors may be outlined as follows:

A. Prehistoric evidence.
   1. Fossil trees and plants.
   2. Laminated clay records.
   3. Fossil pollen (bog records).

B. Historic evidence.
   1. Early travelers' records.
   2. Early surveyors' records.
   3. Local histories.
   4. Contemporaneous writings.

Due to the paucity of prehistoric evidence in the region under consideration, little can be said at present. The historic evidence which I shall present has been largely gleaned from nos. 1, 3, and 4 under B.

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[2] Massachusetts, Rhode Island, and Connecticut.

indebted also, to Dr. M. L. Fernald of the Gray Herbarium, Harvard University, for his kind assistance in supplying data on the location of *Chamaecyparis* bogs. The reference work was largely done at the New York City Library, the Colonial Library at New Haven, the Yale University Library at New Haven, the Southbridge Public Library, the Ferguson Library at Stamford, Connecticut, the Ohio State University Library, and the private library of Mr. F. A. Bartlett, Stamford, Connecticut.

HISTORICAL FACTORS: PRE-COLONIAL

The picture which may be gained from the writings of the early travelers is fragmentary, but at least it gives a basis for surmise as to the character of the forest at the time of settlement by the whites. On one subject, all are in accord and that is the observation that the original forest was, in most places, extremely open and parklike, due to the universal factor of fire, fostered by the original inhabitants to facilitate travel and hunting. We do not know the exact Indian population of southern New England at the advent of the whites, but it was probably about the maximum that could exist under the conditions of the times. Dwight (III, 31) gave an estimate of about 80,000 distributed over an area of thirty to forty thousand square miles. At any rate, there was probably a sufficient population to bring about an annual burning of most of the country sufficiently dry for a conflagration. The burning of the forests and grasslands, it must be remembered, was a universal custom among aboriginal people, not only in the Americas, but in many other regions of the world as well.

To quote from Thomas Morton[3] (1632), "the Salvages are accustomed to set fire of the country in all places where they come; and to burn it, twize a yeare, vixe, at the Spring, and at the fall of the leafe. The reason that moves them to do so, is because it would be otherwise so overgrown with underweedes[4] that it would be all a copice wood, and the people could not be able in any wise to passe through the country out of a beaten path. . . . The burning of the grasse destroyes the underwoods, and so scorcheth the elder trees, that it shrinks them, and hinders their growth very much: So that hee that will look to finde large trees, and good tymber, must not depend upon the help of a woodden prospect to find them on the upland ground; but must seeke for them . . . in the lower grounds where the grounds are wett when the country is fired. . . . For when the fire is once kindled, it dilates and spreads itself against as with the winde; burning continually night and day, until a shower of raine falls to quench it. And this custome of firing the country is the means to make it passable, and by that meanes the trees growe here and there as in our parks: and makes the country very beautifull, and commodius."

Dwight, somewhat more than 150 years later,[5] gives an additional purpose

[3] Chapter XVII. Morton's observations were in east central Massachusetts, in what might be termed the Boston region. He lived until his expulsion from the colonies near what is now Wollaston.

[4] Underwoods?

[5] Many of Dwight's travels took place in the latter part of the eighteenth century and the first part of the nineteenth. His descriptions, however, were not published until 1821.

for the Indian's fires. Although the character of the New England woods had greatly changed by his time as a result of clearing, grazing and other factors incidental to white settlement, he had visited western New York state which had been more recently subject to Indian influence. "The object of these conflagrations was to produce fresh and sweet pasture, for the purpose of alluring the deer. . . . Immediately after the fires a species of grass springs up, sometimes called fire grass."[6] "Of this nature were always the oak and yellow pine grounds: which were therefor usually subjected to an annual conflagration. The beech and maple grounds were commonly too wet to be burned." In Letter VIII, p. 103, the same author states that "The aborigines of New England customarily fired the forests that they might pursue their hunting with advantage . . . the grounds which were covered with oak, chestnut, etc., or with pitch pines, were selected for this purpose, because they alone were, in ordinary years, sufficiently dry. Such, to a great extent, were the lands in New England; and they were probably burned for more than 1,000 years."

This original open type forest is the direct antithesis of the present day type of "brush" or coppice wood which is characteristic of southern New England, and which is partly the result of clean cutting at frequent intervals. As the country was settled, much of the land was completely cleared and cultivated, mowed, or pastured. Many of the old records state that the colonists continued the burning of the woods after the expulsion of the Indians to maintain grass for pasturage in the areas not completely deforested. Progressive clearing of the land for agriculture continued until the early part of the nineteenth century. Between 1820 and 1850 the area of cleared land attained its maximum amounting to 75 or 80 per cent of the total in many southern New England counties. Since the Civil War, there has been a gradual abandonment of this cleared land in many places, and slow reversion to forest. During the seventies, the portable steam sawmill came in, and by the end of the nineteenth century, practically all of the remaining old woodland tracts had been cut. As a result of these two factors, approximately 60 per cent of southern New England is now brush land or young woods, either succeeding the older woods or invading land which was once cleared or cultivated. Woodland trees one hundred years old are scarce, and forests in which the dominant trees are several centuries old, as was the original condition, are practically non-existent.

What do the early commentaries say that would throw light on the original forest types in southern New England? Captain John Smith in his description of southern New England (1616) made the statement[7] "Oke is the chiefe wood." Morton (1632) in his list of trees of New England gives greatest prominence to oak, walnut (hickory), and chestnut. Wood (1634)

[6] Probably *Agrostis hyemalis* (Walt.) BSP.
[7] P. 16.

stated that the "chiefe and common timber for ordinary use is oake and walnut."[8] The latter author gives a description of the early forest which is quoted as follows, inasmuch as in addition to confirming Morton's account, it gives a better idea of the character of the woods: "The timber of the Countrey grows straight and tall, some trees being twenty, some thirty foot high, before they spread their branches; generally the trees be not very thicke, though there be many that will serve for mill posts, some beeing three foote and a halfe o're. And wheras it is generally conceived that the woods grow so thicke, that there is no more cleare ground than is hewed out by labour of man; it is nothing so; in many places, divers acres being cleare, so that one may ride a hunting in most places of the land, if he will venture himselfe for being lost; there is no underwood saving in swamps and low grounds . . . for it being the custome of the Indians to burn the wood in November, when the grass is withered, and leaves dryed, it consumes all the underwood and rubbish, which otherwise would over grow the country, making it unpassable, and spoil their much affected hunting; so that by this meanes in those places where the Indians inhabit, there is scarce a bush or bramble, or any cumbersome underwood to be seene in the more champion ground, small wood growing in these places where the fire could not come is preserved."

Southern New England,[9] except the mountains, was at the time of this narrative, very probably covered with oak-hickory and oak-chestnut on the uplands, while the sandy, so-called "Pine plains" were pitch pine. The climatic climax types (white pine, hemlock, maple, beech) largely composed of trees sensitive to fire, were very probably restricted to the moister areas or to protected ravines and gorges. The extensive annual fires to which the land was subjected for centuries would tend to make the xeric and fire-resistant oaks, the "chiefe wood." That the distribution of the white pine and hemlock in the region designated as the "white pine" area in Figure 1 and the hemlock type in the area in southern Connecticut mapped as the "oak" region, was greatly restricted until a comparatively recent date may be surmised from the following. As late as the beginning of the nineteenth century, Dwight (vol. IV, p. 218) states "that the pine, south of the district of Maine, if it were all collected into one spot, would scarcely cover the county of Hampshire" and that "nine-tenths of all the forests in this country, South of the District of Maine, are composed either of oak, hickory, etc., or of beach, maple, etc."

That most of southern New England was not typical forest, but a woodland greatly modified by fire and anthropeic factors seems quite certain. In addition to keeping the woods open by means of fire, the Indians had undoubtedly cleared certain regions, either for their primitive agriculture or for other reasons. The present site of Boston was reported to have been so

[8] In the old accounts—"walnut" was used synonymously with hickory and does not refer to *Juglans*.
[9] Probably most of the southern New England region, except the Berkshire, Taconic and possibly the hilly region of North Central Massachusetts had been subjected to the fires set by the Indians.

free of forest, presumed to have been cleared by the Indians, that the settlers were forced to obtain their firewood from the wooded islands in the harbor. There were so-called "natural meadows" along many of the streams, and on many of the higher, overdrained sandy or gravelly knolls were open areas dominated by *Andropogon scoparius*, the climax grassland of such sites in southern New England. In addition, there were open brushy plains in certain regions, composed largely of bear oak (*Quercus ilicifolia* Wang.) and sweet fern (*Comptonia asplenifolia* L.), which were the habitats of the heath-hen. While many of these were no doubt kept in this condition by fire, there were undoubtedly others such as the Seekonk plain, in Bristol County, Massachusetts; and the Plainfield area in Windham County, Connecticut, which were edaphic and physiographically similar to the Hempstead plain of Long Island, New York (Harper, 1912). Many of the natural wet meadows may have originated as beaver meadows.

Wood (1634) described the natural meadows: "There be likewise in divers places neare the plantations great broad meadows, wherein grow neither shrub or tree, lying low, in which Plaines growes as much grasse, as may be throwne out with a sithe, thicke and long, as high as a man's middle."

The activities of other native animals may have been important in influencing the original vegetative types. The browsing of great numbers of deer (Rhoads, 1903), the effect of the feeding, roosting and nesting of the millions of wild pigeons (Lawson, 1709), and the great numbers of wild turkeys, both of which fed largely at certain seasons of the year, on acorns and beech mast, were influences which in certain regions may have locally modified the character of the forest.

Fires, in addition to reducing the undergrowth, must have exerted a profound influence on the forest types. Such fire-sensitive species as hemlock, white pine, beech, and juniper must have been greatly restricted in areas where they would otherwise have occurred in abundance. Many other trees as a result of the fire-scorching became hollow, and it is probable that the great number of hollow trees reported in the early woodlands may have owed their condition to this cause.

HISTORICAL FACTORS: THE POST-GLACIAL PERIOD

As the ice mass of the last glaciation slowly retreated from Long Island Sound, the wave of vegetation that followed in its wake undoubtedly roughly corresponded in its successive stages to those which may now be encountered from the tundra southward. It is reasonable to suppose that southern New England was at one time tundra, followed by the boreal forest of spruce and fir, relicts of which now exist on the highest mountains of the north-western and north-central parts. As climatic conditions became less favorable to this type, an invasion of white pine and hemlock very probably occurred and also an infiltration of maple and beech from the west.

As we do not as yet have pollen analyses of peat bogs from New England, we do not know exactly how or when one forest type succeeded another. It is known, however, that in the middle West, a dry period occurred about 3,000 years ago which resulted in a dominance of xeric species, principally oaks. Although there is no present evidence of such a period in southern New England, it is not unreasonable to suppose that such did occur and very probably was the basic reason for the establishment of oak and pitch pine forests which were maintained by the Indians' fires until the white occupancy.

It seems probable also that fires were frequent on dry sites, even before the Indian occupancy. Such fires could have been started by lightning igniting the dead wood in hollow trees which might burn for several days and from the sparks of which a general conflagration could have been kindled. It can safely be assumed that fire has been a constant attendant of dry woods from time immemorial.

Historical Factors: Colonization

During the seventeenth century, white settlement was hampered by Indian hostility and warfare, but this factor once removed, colonization went on rapidly. By the middle of the eighteenth century, settlements existed in all of the present counties, and most of the present townships. The woodlands were completely cleared over large areas; while in others, cessation of the Indian fires had resulted in a heavy undergrowth. Other woodlands were still burned by the settlers to keep them open for grazing. In many places woods were completely cleared for pasturage. This was done by felling the larger trees in June and burning the tangled windrows when the leaves had dried in late July or August. As settlement progressed, more and more of the entire region was fenced in with stone fences, making a marked and abrupt division between woodlands, pastures, fields, and cultivated grounds.

Much of the wealth of the settlers lay in their cattle and sheep, and the intense grazing to which a large part of the region was subjected for over 150 years had a profound effect upon the vegetational types, as will be described later.

Exploitation of the woodlands kept pace with the agricultural development. During the latter part of the seventeenth century and the early part of the eighteenth, the pitch pine forests were worked for tar, turpentine, and lampblack, which were exported to Great Britain. Temple (1889) in his history of Palmer, Massachusetts, in describing the early settlement of the region, states that as a means of raising money, "these first-comers to the Elbow Tract made considerable turpentine and tar. The pitch pines, which were then the old growth on our plains, were 'boxed'," while "candlewood" was obtained from the pitchy knots.

Pitch pine was an important source of fuel for the colonists and later,

during the early half of the nineteenth century, great quantities were consumed for fuel by the wood-burning locomotives. Emerson (1846) states that "pitch pine is preferred to any other wood in the northern states as fuel for steam engines and vast quantities of it are also consumed for the supply of families." The estimated annual consumption by the Massachusetts railroads at that time was 53,710 cords, which was almost entirely pitch pine.

The oak and hickory woods were also, as at the present time, largely cut for fuel. The sprouting of these trees after cutting perpetuated the "sprout lot" of the farmers. Dwight in 1821 (Vol. I, p. 80) states "when a field of wood is, in the language of our farmers, cut clean, i.e., when every tree is cut down, so far as any progress is made, vigorous shoots sprout from every stump, and having their nourishment supplied by the roots of the former tree, grow with a thrift and rapidity never seen in stems derived from the seed. Good grounds will thus yield a growth, amply sufficient for fuel, once in fourteen years."

Where white pines occurred, these were prized above every other tree for masts. In fact, one of the early names for the white pine was "mast pine." Regarding restrictions on cutting this species, Belknap (1792) in his History of New Hampshire (Vol. III, p. 81) states that "before the revolution all white pines (excepting those growing in any township granted before the 21st of September 1722) were accounted the King's property, and heavy penalties were annexed to the cutting of them, without leave from the King's surveyor."

THE PRINCIPAL FOREST REGIONS

The preceding has dealt largely with the historical factors. This evidence may now be compared with what present day ecology offers.

For convenience, southern New England may be divided roughly into the following regions:

(1) The Oak Region, (2) The White Pine Region, and (3) The Northern Forest Region.

These terms are employed for simplification and do not imply that, for instance, the white pine region is solid white pine forest, but simply that the region mapped is characterized by an abundance of white pine. These regions, outlined in Figure 1, correspond, to a great extent to the classification adopted by the New England Section of the Society of American Foresters, except that they give Cape Cod a distinct classification, termed "Pine and Oak Region," while what the writer calls the "Northern Forest Region" is termed the "Spruce and Northern Hardwood Region."

Furthermore this classification does not imply that the terms refer to the climatic climax type for the region, the occurrence of which in each region will be discussed later.

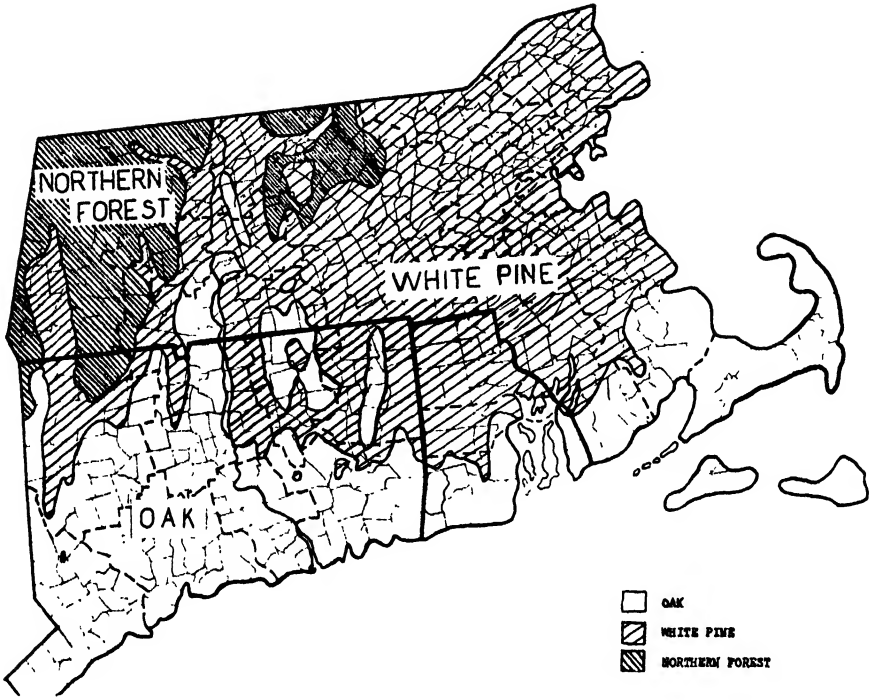

Fig. 1. The principal Forest Regions of southern New England. Approximate boundaries.

1. THE OAK REGION

This occupies a large part of Connecticut, southern Rhode Island, and southeastern Massachusetts, and is characterized by the dominance of oaks and the absence or scarcity of white pine. Originally a large part of the better drained soil, land which was largely cleared for agriculture, was oak-hickory, while oak-chestnut predominated on the drier ridges and south slopes. The upper portions of the steeper ridges were undoubtedly, as they are today, characterized by chestnut oak (*Quercus montana* Willd). The chestnut (*Castanea dentata* (Marsh.) Borkh.) has of course within the past twenty-five years been practically exterminated as a forest tree by the chestnut blight (*Endothia parasitica*). The swamps were largely red maple (*Acer rubrum* L.)—elm (American elm, *Ulmus americana* L.)—pin oak (*Quercus palustris* Muench.), the latter oak in southwestern Connecticut characteristically overtopping the forest. Swamp white oak (*Quercus bicolor* Willd.) was a component here also, while black gum (*Nyssa sylvatica* Marsh.) occurred in most of the swamps of the entire oak region. The principal oaks are the white (*Quercus alba* L.), black (*Quercus velutina* Lam.) and red (*Quercus rubra* L.); the two latter becoming less abundant in the eastern part where scarlet oak (*Quercus coccinea* Muench.) becomes numerous, par-

ticularly in southeastern Massachusetts where it is frequently the predominating species.

The lower better-drained soils arising from the swamps, and also the sheltered rocky ravines and north slopes were dominated by the typical mixed mesophytic forest (Figure 2), originally composed of oak, chestnut, hickory (*Carya ovata* (Mill.) K. Koch and *C. glabra* (Mill.) Spach.), sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.), tulip poplar (*Liriodendron tulipifera* L.), which characteristically overtopped the forest, and a varying admixture of eastern hemlock (*Tsuga canadensis* (L.) Carr.). This type probably represents the climatic climax of the region. Black or sweet birch (*Betula lenta* L.) is common in this type and where clean cutting occurs is apt to come in abundantly and form a secondary type together with an increase in oaks. In southwestern Connecticut, sweet gum (*Liquidamber styraciflua* L.) is an abundant component of the forest near the coast.

The successional types in this region have been very well worked out by Lutz (1928) who found that the common "old field" associations such as red cedar (*Juniperus virginiana* L.), gray birch (*Betula populifolia* Marsh.), pin cherry (*Prunus pennsylvanica* L.f.), choke cherry (*Prunus virginiana* L.), red maple, black birch and dogwood (*Cornus florida* L.) occurring in varying admixtures are succeeded by hardwoods, such as oak, hickory, white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.) and sugar maple, tending toward the hemlock-hardwood climax.

Succession on old fields and open land depends to a considerable extent on the site, and its relation to the position of light or wing-seeded trees. Gray birch is one of the first to come in as a rule, although abandoned upland mowings frequently show an abundance of choke cherry or pin cherry; lowland mowings revert to red maple or alder (*Alnus incana* (L.) Moench. and in some places *A. rugosa* (DuRoi) Spring). Pastures usually become heavily stocked with red cedar. Succession on cut-over lands may be further complicated by the occurrence of fire.

For many years, repeated "clean" cuttings favored chestnut, due to its outstanding ability to sprout and its rapid early growth, but the chestnut is now no longer important in forest ecology. There is a tendency for oaks to increase following cuttings, even in the mixed mesophytic types, which types, especially the hemlock associations, clean cutting practically destroys. Hemlock, although originally restricted by fires, occurred locally throughout southern New England, except possibly in the Cape Cod region, growing principally in ravines, gorges, north slopes and protected swamps and low moist sandy grounds. Theoretically it is the tree best fitted to dominate the climax forest of southern New England, due to its longevity, shade tolerance and ultimate size. On the other hand its susceptibility to fire and drying winds, and its rather high moisture requirements render it poorly adapted to

such xeric sites as south-exposed ridges and such sandy, level, wind-swept coastal regions as Cape Cod.

The Cape Cod region was originally partly oak forest on the better soils, pitch pine *(Pinus rigida* Mill.) on the lighter, sandy soils, and oak-pitch pine in the tension zone between the two. Dwight, 1821 (Vol. III, pp. 74-109) states that the woods from Wareham to Sandwich were of "yellow pine" with oaks interspersed at New Bedford and Rochester; from Orleans to Eastham, first "oaks," then "oak and pine" to Wellfleet and Truro. From Truro to Provincetown there were no woods but "whortleberry bushes and small oaks." From Sandwich to Plymouth were "yellow pine" plains. The region from Truro to Provincetown were originally wooded, to judge from Gosnold's account[10] "that the Pilgrims in 1620 found Cape Cod harbor compassed about to the very sea with oaks, pines, juniper, sassafras and other sweet wood." Nantucket was also reported to have been originally wooded with oak, hickory, pine and other trees (Chrysler, 1905). The complete destruction of forest in these places was due to cutting and grazing.

In northwestern Ohio, in the sandy regions near Lake Erie and western New York state in the Batavia region, were areas known as "oak openings," sandy areas supporting a scattered open growth of oaks intermingled with grass *(Andropogon scoparius)*. A somewhat analogous condition exists on the sandy plains of North Haven, Connecticut, where there are areas of open sand. This condition has existed for a very long time. Dwight (1821) mentions it in his *Travels* (Vol. II, p. 30), stating that the soil "near the northern limit of the township is so light as in two or three places of small extent to be blown in drifts. In these places it is absolutely barren." (See Nichols, 1914.)

2. THE WHITE PINE REGION

This region is at present dominated by northern white pine *(Pinus strobus* L.) which although exceeded numerically by many other trees, is a striking feature of the landscape due to its height and evergreen appearance. The young trees are easily killed by fire and originally the species was undoubtedly much restricted by this factor. At the time of settlement it was probably abundant only in swamps; low, moist sandy areas (known as "pine flats"); and on exposed ridges. Where white pine occurs farther south in isolated stations in the oak region of southern New England, the sites are almost invariably exposed ridges, where competition with the more rapidly growing young hardwoods is less keen. Second growth stations of white pine in the oak region occur only where plantings have been made or where pastures or openings have seeded in from older trees, either planted or relicts on exposed areas.

The greater part of the area mapped as the white pine region was during

[10] Quoted in Freeman, F. *History of Cape Cod*, p. 62. Requoted by Chrysler (1905).

the Indian occupation probably oak-hickory on the lower slopes and better drained uplands, and oak-chestnut on the drier ridges and slopes, with only scattered white pines or groups of white pines overtopping the woodland. Even the so-called "pine flats" were probably not pure white pine, but white pine with pitch pine or hemlock, or in the swamps, with red maple and yellow birch (*Betula lutea* Michx.) as an understory.

However, the great height of the white pine, with scattered trees dominating the forest, gave the impression of greater abundance than was really the case. The white pine was by far the tallest tree in the original New England forest, and so impressed the early travelers. Michaux stated that it was the loftiest and most valuable of the productions of the North American forest. "Its summit is seen at an immense distance, aspiring to heaven, far above the heads of the surrounding trees." Its size may have been exaggerated, although the largest trees were cut early in the history of the country and we have no definite method of ascertaining exactly the proportions which the white pine may have reached. At least we do not have today any white pines of 250 feet in height and 6 feet in diameter as recorded by Dwight (1821, Vol. I, p. 36) or 264 feet, as a Lancaster, New Hampshire, tree was reported to have been; or the trees at Blandford, Massachusetts, said by Emerson to have been 223 feet in height. Probably, however, some of the very large trees in the original forest reached a height of 200 feet. In 1841, a 90 foot mast from the Penobscot Valley in Maine measured 36 inches in diameter at the butt and 28 inches in diameter at the top. Michaux recorded two trunks near the banks of the Kennebec, "one of which was 154 feet in length and 54 inches in diameter; the other 142 feet in length and 44 inches in diameter."

An interesting portrayal of the white pine forest is given by Jeremy Belknap (1812, Vol. III, Chapter VI, p. 56). "Notwithstanding the gloomy appearance of an American forest, yet a contemplative mind may find in it many subjects of entertainment. The most obvious remark, is the silence which reigns through it. On a calm day, no sound is heard but that of running water, or perhaps the chirping of a squirrel or the squalling of a jay. Another thing, worthy of observation, is the aged and majestic appearance of the trees, of which the most notable is the mast pine. This tree often grows to the height of 150 and sometimes 200 feet. It is straight as an arrow, and has not branches but very near the top. It is from 20-40 inches in diameter at its base and appears like a stately pillar, adorned with a verdant capital in form of a cone. Interspersed among these are the common forest trees, of various kinds, whose height is generally about 60 or 80 feet. In swamps and near rivers, there is a thick growth of underwood, which renders traveling difficult. On higher lands, it is not so troublesome; and on dry plains it is quite inconsiderable."

An account of a pitch pine-white pine-hemlock forest is given by Wilson Flagg (1890, pp. 226 and 304). He speaks of the pitch pine thus: "Some of the ancient pine woods in New England were made up principally of this species. Such was that extensive wood near Concord, New Hampshire, known by the poetic appellation of 'Dark Plains,' and in the early part of the century occupying a wide, flat region in the valley of the Merrimack river." "I watched the scenes as we rode slowly by them,—the immense pillars that rose out of a level plain, strewed with brown foliage, and interspersed with a few bushes and straggling vines; the dark summits of the white pines that rose above the round heads of the other species which were the prevailing timber; the twilight that prevailed these woods even at high noon; and I thought of their seemingly boundless extent, of their mysterious solitude, and their unspeakable beauty."

While the two preceding descriptions refer to regions just outside that considered in the present work, they would undoubtedly apply to certain restricted areas in Massachusetts and northern Connecticut and Rhode Island encountered by the original settlers. Wood (1634) stated that he had "seene of these statly high groune trees, ten miles together, close by the River side, from which by shipping they might be conveyed to any desired port." Morton (1632) listed an "infinite store" of pine in "some parts of the country. I have traveled ten miles together where there is little or no other wood growing." Such might, however, have referred to pitch pine.

The climatic climax in this region is probably white pine-hemlock. The original extensiveness of the oak-chestnut-hickory pine type may have been due to the prevalence of fire, or it may have been even edaphic on the drier sites. The occurrence of white pine in the climax, despite its low tolerance of shade, may be explained on the basis of the following factors: 1. The enormous amount of seed that may be set by an individual tree. 2. The wide scattering of the winged seeds and its rapid growth in openings in the forest, caused by windthrows, or fires. 3. Its great height, normally overtopping the forest 10 to 40 feet or more. 4. Its rapid growth, upward through gaps in the forest canopy in an open woodland. Once above the foresty canopy its position is secure. 5. Its longevity. Spaulding records white pine 400 years old. 6. The crashing of the aged trees, opening up spaces in the forest. 7. The greater ability to withstand ice storms and heavy snows which are more destructive to oaks and other hardwoods.

The present abundance of pure white pine stands in this region is due largely, as stated by Dana (1930), to its ability to take possession of abandoned farm lands. When these pure stands are cut clean, as they generally are after 30 or 40 years, they revert to a secondary type of deciduous trees in varying proportions, unless pastured. When pastured, white pine generally becomes reëstablished, if there are neighboring seed trees. As the prin-

cipal monetary value of the southern New England woodland lies in white pine[11] for lumber, and oak and birch for fuel, they are so managed. In the oak and birch types of woodland there is a regeneration due to sprouting, unless pastured; in the white pine stands, regeneration *does not* take place, *unless pastured.* Cleared pastures in this region almost invariably revert to white pine or gray birch, both trees frequently becoming established while pasturing is continued. Old fields are occupied by the same species, although on overdrained and sandy sites pitch pine or aspens are frequently the pioneers. Where pasturing does not occur, the grass *Andropogon scoparius*, a species quickly destroyed by grazing, has a tendency to dominate in such sites and produces a "prairie" (see photo by Nichols, 1914, p. 188), which greatly delays reforestation, particularly if burned. In meadows and low mowings, red maple and alder are likely to be abundant, although white pines will frequently become established and eventually dominate the stand.

Where an old white pine-hemlock forest has been cut clean, this type is succeeded by a mixture of such trees as sugar maple, white ash, basswood, yellow and other birches, particularly in the northern part of the region. In the southern part, oaks are more likely to come in, particularly where the stand has been largely white pine. In many cases an understory of young oaks becomes established in a white pine grove, before cutting of the pine, and is thus ready to take its place when the pine is removed. The following observations were made on such a grove at Southbridge, Massachusetts.

1910. A grove of white pines about 70 years old which had evidently seeded in from an old "cabbage" pine in the corner of the lot, about 130 years old. Most of the trees were 70 to 80 feet high and 20 to 36 inches in diameter. Fifty or 60 years before, this grove was evidently surrounded by pasture or meadow land. The floor of the woodland had been burned over repeatedly producing a grassy condition.

1911. Fires ceased.

1912. Young "brush" mowed out by scythe.

1915. Canada mayflower, false solomon seal, solomon seal and other herbaceous plants in great profusion; asters and golden rod in the autumn.

1918. An undergrowth of oaks 2 to 5 feet high. Fire scars still present on some of the pines.

1928. Heavy oak undergrowth 5 to 20 feet high. Thick oak and pine leaf litter, obliterating grass and herbage which was characteristic

[11] A small group of sentinel pines, the tallest and oldest white pines in the locality, towering high above a woodlot overlooking the Quinnebaug valley near the Massachusetts-Connecticut line at Dudley, Massachusetts, had been a prominent land mark since the memory of the oldest inhabitants. These trees, previously estimated, ranged from 100 to 125 feet in height. The woodlot in which they occurred was cut in the autumn of 1931, and on May 22, 1932, diameters and ring counts of some of the larger stumps, which had been cut about a foot from the ground, were: 48 inches, 198 rings; 41 inches, 191 rings; 36 inches, 173 rings; 39 inches, 157 rings. Contrast with this, a white pine stump in the fire-swept Douglas woods, described later. This stump, a foot from the ground, measured 20 inches in diameter and showed 151 rings.

a dozen or more years previous. The old fire scars on the pines practically overgrown in most cases.

3. THE NORTHERN FOREST REGION

In the mountainous areas of western and north central Massachusetts, a type quite different from the preceding occurs. Although white pine is occasional and hemlock abundant, the bulk of the forest is what is known to foresters as the northern hardwood type, consisting largely of yellow birch, white birch, sugar maple and beech; with white ash and basswood abundant in certain areas. Originally the physiographic areas were very well marked and no doubt corresponded to the condition in Vermont which was classified by Thompson (1824, p. 26):

1. Alluvial areas—oak, butternut, elm, walnut (hickory), chestnut.
2. Higher flats—"Pine."
3. Medium uplands—Sugar maple, beech, birch, ash, basswood, elm, butternut, cherry, hornbeam, spruce, hemlock.
4. Sides and summits of mountains—Hemlock, spruce, fir.

Intensive cutting as well as other factors incidental to settling greatly disturbed the original condition. Cutting as usual destroyed the conifers. Second growth stands are apt to be characterized by a greater per cent of yellow birch, white birch, striped maple, pin cherry, and aspen than the original.

On the higher altitudes, red spruce and balsam fir predominate and originally formed nearly pure stands with a characteristic undergrowth of moosewood and hobblebush. Clean cutting throughout the area generally results in the possession of the land by northern hardwoods, particularly birch; while the old pastures and abandoned fields revert to conifers. Annual fires probably did not occur in this region as was the case farther south, although occasional fires in dry seasons occurred, destroying the spruce-fir types over large areas and initiating the succession of fireweeds, aspen, pin cherry and birch with eventually the conifers again invading and finally dominating.

In this region the climatic climax types were undoubtedly the spruce-fir (Fig. 2) on the higher altitudes, and hemlock-hardwoods of the type described by Lutz (1928) on the lower slopes. A virgin forest, the last of its kind in Connecticut, occurring at Colebrook until 1912 when it was cut, was undoubtedly of the latter type and represented the climax which at one time probably clothed the greater part of the Berkshire hills. Fortunately an accurate census of this tract was made by Nichols (1913) before it was destroyed. To quote Lutz's summarization, it was "characterized by the predominance of hemlock and beech. On the whole these two species were about equally abundant and taken together, comprised at least 55 per cent of the stand. The relative proportions of the two were found to vary, but almost

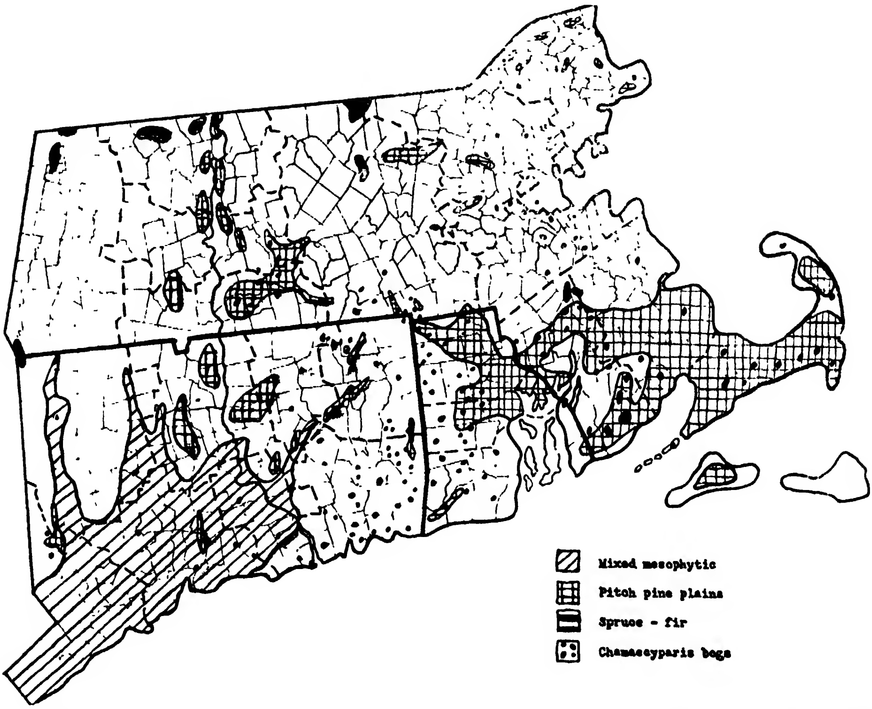

FIG. 2. Locations of certain forest types in southern New England. Approximate boundaries.

without exception one or the other was dominant. The remainder of the forest was made up approximately as follows (in per cent of the total number of trees): sugar maple, 12; yellow birch, 10; red oak, 6; chestnut, 6; white ash and basswood, 7; black cherry (*Prunus serotina* Ehrh.), red maple, black birch, and white pine, 4." Beech-maple, pure sugar maple stands and spruce-hardwoods, as physiographic climaxes, undoubtedly originally occurred in places, the two former on the drier upper slopes or tops of the lower hills and plateaus, and the latter in the tension zone between the spruce-fir of the higher altitudes and the hemlock-hardwoods of the moist slopes. On overlydrained dry ridges, oaks and chestnut also occurred.

CERTAIN PHYSIOGRAPHIC TYPES IN NEW ENGLAND

1. Flood Plain and Alluvial Woodland Associations.

A characteristic flood plain association occurred along most of the larger streams in southern New England, more extensive probably along certain portions of the Connecticut and Housatonic rivers than elsewhere. American elm and sycamore (*Platanus occidentalis* L.) were general, with silver maple (*Acer saccharinum* L.) and red maple abundant in some places. River birch (*Betula nigra* L.) was local and scarce as was also hackberry (*Celtis occi-

dentalis L.). The sand bars and sandy banks were dominated by cottonwood (*Populus deltoides* Marsh.) and willow (*Salix* spp.).

Edaphic meadows, some of which were of great extent, also occurred in the river valleys and were known as Intervales. According to Dwight, these were most extensive at "Wethersfield, Hartford, Windsor, Glastonberry, East Hartford, and East Windsor in Connecticut; Longmeadow, Springfield, Northampton, Hadly, Hatfield, Sunderland, Deerfield and Northfield in Massachusetts." Brimfield and Brookfield, Massachusetts, both had extensive natural meadows.

Great woodlands also occurred on the alluvial soils and were composed of many of the species listed above with a greater admixture of red oak, chestnut, hickory, white ash and particularly butternut (*Juglans cinerea* L.). In the white pine region, this pine was also an abundant component of the alluvial forest.

2. Pine Plains.

The pine plains (Fig. 2) so frequently mentioned by the early writers were for the most part composed of pitch pine, although in the white pine region there tended to be an admixture of white pine and even hemlock, particularly in the lower moister areas. In the southern and southeastern parts there was a tendency to oaks, particularly scarlet, white and black. The pine plains were invariably on light, sandy soil. The abundance of pitch pine was probably due to the frequency of fire which favored this fire-resistant species by destroying the humus and eliminating competing species. With the fire factor removed, there is a tendency for white pine and hemlock to supplant the pitch pine in the northern area, and for oak or pitch pine and oak to dominate on these plains in the southern part. The pitch pine forests were early exploited and disappeared over a considerable portion of their original range. Cutting is particularly disastrous to conifers, due to the inability of most to sprout, and the cutting of the pitch pine woods almost invariably resulted in a replacement by oak. Dwight (1821, Letter XXXI, p. 39) observed "From Windsor the road, leaving the Connecticut River proceeds to Suffield over a plain of yellow pines, about five miles in extent. At the entrance upon this plain, the pines for near a mile were, many years since, entirely cut off: and in their place has sprung up a forest of oaks." He also spoke of Montague, Hatfield, Ware, Ludlow, Palmer, Sandwich and Plymouth, Massachusetts, as being characterized by extensive "yellow" pine plains. Letter L, p. 2, stated "Immediately after we left Plymouth we ascended the brow of a vast, yellow pine plain, spreading over the greater part of the county of Plymouth, a part of the county of Bristol and a part of the state of Rhode Island."

Some of the higher over-drained gravelly plains were, however, destitute of large trees from the earliest times. The difficulties of the early settlers at Concord, Massachusetts in 1635 were described in Johnson's "Wonder-work-

ing Providence" (Barber, 1848, p. 378). Much of the land was composed of "ragged plains," largely "shrub oak" and sweetfern, making traveling very difficult.

3. Chamaecyparis Bogs.

Scattered peat bogs bearing a growth of southern or coast white cedar (*Chamaecyparis thyoides* (L)BSP.) occur through the southern and eastern area of southern New England, invading stagnant pools and lakes (Fig. 2). Particularly in the more northerly located bogs, there is a fringe of tamarack (*Larix lariana* (Du Roi) Koch.) and black spruce (*Picea mariana* (Mill.) BSP.) at the edge of the water, the thick growth of cedar supplanting this type farther back. The *Chamaecyparis* is undoubtedly an evanescent type, being succeeded, as the swamps dry out, by the deciduous swamp forest in the oak region, and by white pine-hemlock in the white pine region. Clean cutting completely destroys the cedar type, red maple and yellow birch succeeding it. Sphagnum moss, pitcher plant (*Sarracenia purpurea* L.) and poison sumac (*Rhus vernix* L.) are common associates in the more open spots, with *Caltha palustris* growing in the shaded pools. In southeastern Connecticut, there is frequently a heavy undergrowth of *Rhododendron maximum.*

4. Maple Swamps.

Most of the swamps in southern New England are characterized by the presence of red maple. While there were undoubtedly many maple swamps originally, it is probable that most of those at the present time represent a secondary condition. The cutting of the white pine and hemlock in the swamps of the white pine region has left the red maple and yellow birch to occupy the site sometimes to the complete exclusion of the original dominant species; while in the oak region, the swamps which are now red maple, black gum (*Nyssa sylvatica* Marsh.) and elm, undoubtedly contained much more pin oak than occurs today. In old growth swamps in this region the pin oak almost invariably overtops the elm and maple, while the swamp white oak was also a dominant species. Probably the oaks and the white ash dominated the better sites, restricting the pure stands of elm and maple to the least drained situations.

EFFECTS OF PASTURING

Two centuries of pasturing have had a profound effect upon the vegetation of southern New England, although the country is not nearly so extensively pastured as it was 75 or 100 years ago. At that time the pastures were largely kept cleared of "brush" by means of the scythe and "grub hoe." This brush was composed principally of shrubs or young trees of species distasteful to cattle. As stock raising waned, many of the pastures were left idle and allowed to revert to brush and forest. In the white pine region, this became profitable to the farmer, who was able to realize on the young white

pine timber which quickly took possession of such sites. The larger trees coming in on pastured land in New England are almost invariably conifers. As a rule these are not browsed by cattle. The destruction of the young hardwoods by grazing has thus, by eliminating competition, favored the conifers.

In many parts of the oak region, particularly in western Connecticut where the soil is less acid, red cedar is an abundant invader of pastures. Originally, due to its low tolerance of shade, slow growth, and susceptibility to fire, this species was confined to exposed rocky ridges, protected open borders of swamps and along the seacoast. In the white pine region, the white pine frequently forms pure stands on pasture sites, while in the northern forest region where spruce and fir occur, these species are most likely to reclaim pastures on the higher land. In hilly regions, pure stands of hemlock frequently claim protected, pastured, north slopes; while in sandy regions, the pitch pine is a frequent pioneer. East of the Connecticut River, the patches of *Juniperus communis* are frequently indicative of former sheep grazing.

Probably the original grassland on the higher sandy or gravelly sites was almost pure *Andropogon scoparius.* This species is destroyed by grazing, its place being taken by shorter grasses. If grazing is abandoned, *A. scoparius* quickly becomes reëstablished. Along railroad rights-of-way which are frequently burned, *Andropogon scoparius* is the dominant grass.

Among the shrubs and small trees invading pasture land, may be mentioned the gray birch, which is abundant throughout southern New England, as well as species of *Vaccinium* sp., *Rhus* sp., and *Myrica* sp. *Comptonia asplenifolia, Juniperus communis,* and *Baptisia tinctoria* which are abundant pasture species in many localities east of the Connecticut River, while *Potentilla fruticosa* may spread over moist pastures on the higher lands of the Berkshire and Taconic ranges.

Examples of Old-Growth Forest

1. Oak Region.

It seemed an almost impossible task to locate any woodland of even very limited extent which would at all approach original conditions. I eventually found a small tract near Stamford, Connecticut, which because of its proximity to a railroad had been burned over annually for a great many years, was not subject to grazing, and the trees were of relatively great age. Black oak, white oak, hickory, and sweet gum dominated and stood far apart. Flowering dogwood formed a scattered understory. There was no underbrush. A ring count on an oak stump showed somewhat over 200 years. Evidently the trees were old, but due to the dry site and prevalence of fires had grown slowly. The larger trees were 60 to 75 feet in height. Many were hollow or showed extensive fire scars. This was particularly true of the few beech, maple, elm, and pin oak which existed in the grove. The other oaks and hickories as a rule did not show fire scars (Figs. 3 and 4).

FIG. 3. Oak-hickory woodland, Stamford, Connecticut, subject to annual fires, resulting in an open stand free from underbrush.

(Photo by Dr. R. P. Marshall)

FIG. 4. Same grove as in Fig. 3, showing fire scars on beech. The ground cover near the ledge is largely *Dicentra cucullaria* (L) Bernh.

(Photo by Dr. R. P. Marshall)

In direct contrast to this grove was an original hardwood grove north of Stamford, which had probably not been pastured for many years (Fig. 5). The trees were much larger and the average age may have been slightly greater. Although the large trees stood far apart, there was a dense undergrowth of sweet birch, *Cornus florida, Viburnum,* greenbrier (*Smilax* sp.) and others. Fires had only rarely occurred as evidenced by the dense undergrowth. This grove shows an interesting transition from swamp to upland condition; that is from the swamp type with pin oak, red maple and elm, through mixed mesophytic beech, sugar maple, oak, and tulip poplar (the latter overtopping the forest) to oak-hickory on the higher ground and oak-chestnut (the latter now dead) on the steep, drier slope. There is no hemlock in this grove.

At Laddin Rock, near Stamford, is an old grove of hemlock and mixed mesophytic woodland (Fig. 6). This is in a protected ravine and many of the trees are 200 years or more old.

2. White Pine Region.

An interesting old tract, formerly occurring in this region and known as the Lawson lot, was located near the Woodstock-Union township line in Connecticut. Largely white pine-hemlock, a very interesting transition was shown from swamp to high dry ridge. This grove was dominated by white pine, whose crests overtopped the rest of the forest ten to forty feet, their jagged crowns outlined against the horizon, producing a landmark recognizable for miles around. The swamp sites were largely forested with white pine, hemlock, yellow birch, red maple, and elm. Large sugar maples and red oaks were scattered through the grove on the slightly higher ground; while chestnut, red oak, black oak, white oak, and sweet birch occurred on the higher, drier slopes. White pine was omnipresent; the hemlocks were everywhere also but most numerous in the ravines. This was a wild-appearing woodland. Local inhabitants claimed it to be original forest. There were no signs of fire, pasturing, or cutting. The forest floor was spongy with vegetational debris, and windthrown trees extended their great lengths along the ground. Moss-grown and lichen-covered trunks of standing trees gave the impression of great age, while on the lower slopes great banks of mountain laurel 7 to 15 feet high added to the wildness of the scene. The writer first visited this region in 1917. It was a windy April day and in travelling through the woodland, one was impressed by the fact that although it appeared calm down in the woods, the tops of the great pines were swaying, and the silence was broken by the creaking and groaning of rubbing branches and the roar of the wind through the evergreen tops. The writer was unable to make accurate estimates of the heights of the trees, although he suspected that some of the taller pines may have been 120 feet in height, some of the hemlocks exceeded 90, while the average height of the oaks and chestnuts was

FIG. 5. Oak-hickory woodland, Stamford, Connecticut, not subject to frequent fires. The large trees stand far apart but there is a dense undergrowth. The black oak in the foreground is 114 feet in height.
(Photo by Dr. R. P. Marshall)

FIG. 6. Laddin Rock near Stamford, Connecticut; Hemlock grove in mixed mesophytic woodland. The deciduous tree in the right foreground is a red maple. A few beech are discernible in the grove. Undergrowth has probable been artificially removed. The tallest hemlock in the foreground is about 100 feet in height.
(Photo by Dr. R. P. Marshall)

70 to 80 feet. The trees of largest diameter were red oaks and chestnuts, some of the latter being nearly 5 feet through the trunk near the base. The young growth was largely hemlock. This led the writer to suspect that the predominance of the evergreens might have been a recent development, and that in colonial times the area might have been an open oak-chestnut woodland, particularly as in a part of the woods which had just been felled, it was impossible to find a pine stump showing more than 150 rings. Some of the oaks were over 200. This whole region was cut over a few years after the World War, and every vestige of the conifers destroyed. When the area was revisited in 1931, the predominating trees of the second growth were birch and sugar maple. The latter had seeded in from old maples which had been left standing. A few years prior to cutting, most of the chestnuts had succumbed to the blight.

A somewhat similar tract, in which the pines are much older and larger, is a white pine-hemlock grove at Cornwall, Connecticut, known as the Cathedral Pines (Figs. 7 and 8). Scattered through this grove are large beech, red oak, and sugar maple. There are also chestnuts, but these have now been killed by the blight. The tallest pines here are about 140 feet in height, and judging by the number of rings on a windfall, some of them may be 200 to 300 years old.

The so-called Gulf woods near Southbridge, Massachusetts, long since cut off, were, according to local tradition, largely white pine, hemlock, with here and there large oaks, chestnuts, and beech trees.

The famous Douglas woods, a large tract between Douglas and Webster, Massachusetts, lying on sterile rocky ground, has been cut over at frequent intervals and is now largely low "brush" of young scarlet oak, black oak, and white oak sprouts. Twenty years ago there was considerable chestnut and when I visited the region in 1916, in a tract where the woods seemed the oldest, white, scarlet, and black oaks predominated with scattered white pine and chestnut; and considerable pitch pine in the sandier areas. The swamps were largely white pine, red maple, and yellow birch, with several *chamaecyparis* bogs. This is still a fire-swept area. At the writer's first visit, he thought that originally it may have been predominantly white pine and hemlock, and that frequent fires and repeated cutting had contributed to the destruction of this type. However, the Indians' fires had undoubtedly swept the region long before white settlement and it is probable that in colonial days the distribution of the various forest trees did not differ greatly from that of the present time. Dwight visited the region in the latter part of the eighteenth century and to quote his account: "In the Southwestern part of this township is a large tract of forest known by the name of the Douglas Woods. The trees which are of oak, chestnut, etc., are of moderate size and prove the soil to be indifferent. In the year 1805, when I passed through this

FIG. 7. White pine-hemlock at Cornwall, Connecticut. The tallest white pines are about 140 feet in height.
(Photo by Dr. R. B. Gordon)

FIG. 8. Hemlock ravine in same grove as Fig. 3. The tallest hemlocks are about 100 feet tall.
(Photo by Dr. R. B. Gordon)

region again, I perceived that the inhabitants had begun to make serious depredations on this tract." Dwight's route through the Douglas woods was the old Boston-Hartford stage road from Douglas to East Thompson. Due to repeated cuttings at frequent intervals, this particular part of the region is now largely scarlet oak and bear oak scrub. In the very few relict patches of old trees, the undergrowth on the drier sites is slight and composed mostly of low species of *Vaccinium*.

At South Pond near Brookfield, Massachusetts, on a sandy bluff extending into the lake, known as the Point of Pines, is a very interesting bit of woodland. When I first visited the spot in 1918, the blight had not yet killed the chestnuts, which were the most massive trees scattered through the grove. There were a number of white and red oaks of considerable size and age while scattered white pines, one of which was considerably over 100 feet in height, overtopped the stand. There were a number of very tall pitch pines also, 80 to 90 feet high, but most of the understory was composed of hemlocks of varying ages. The cleared land and pasture east of the grove had seeded in heavily to white pine, with a few of the more sandy spots to pitch pine.

3. The Northern Forest.

A beautiful example of the northern forest still exists in the State Park at Mt. Graylock in the northwestern corner of Massachusetts. The spruce-fir forest is in a natural condition and is one of the most strikingly beautiful groves left in Massachusetts. The grove referred to is that which occurs on the west side of the peak, on the upper slope at the camping ground toward the "Hopper." Most of the stand is red spruce. Balsam fir, canoe birch and a scattering of other northern hardwoods also occur. The trees are tall and straight and give the impression of great age. Some of the taller spruces may be 90 feet or over in height. The undergrowth is rather sparse and is largely hobble bush and striped maple.

Ages of Forest Trees in This Area

Oaks are noted for their longevity, but it is doubtful whether any of our species, even if allowed to live, would attain the age (the proverbial 900 years) of European species. The white oak probably reached the greatest age of our trees under original conditions. The famous Charter Oak at Hartford, Connecticut, presumably a white oak, destroyed by a windstorm on August 21, 1856, was estimated as 1,000 years old, but as it was hollow and no accurate ring count could have been made, this estimate is no more than a guess. *The New England Farmer* (Vol. IV, p. 242) in 1826 recorded its girth at the ground as 36 feet, making it easily the largest oak of which we have record in New England. Sycamores attain a relatively great age, and the large tree at Sunderland, Mass., has been estimated as 500 years of

age.[12] Probably hemlock commonly attains the greatest age of our forest trees. A tree cut on the Holyoke range in 1922 showed over 400 rings. Frothingham (1915) reports hemlocks of 500 to 600 years old. The white pine although a relatively long-lived tree, probably did not ordinarily attain this age. Trees 400 years old have been recorded.[13] One of the oldest white pines in southern New England was the famous "Bear Tree" in Palmer, Massachusetts. This tree was cut about 1921. When I saw it in 1919 it was hollow and badly infested with carpenter ants. I described it in my notes as a triple-leader tree, branching about 20 feet from the ground, 100 feet in height, and about 5½ feet in diameter at the base. It gained its name from the tradition that in the days of early settlement, about 175 years before, a black bear was shot out of the lower branches.

Some specimens of *Chamaecyparis thyoides* in the cedar bogs were reported to be old. Their growth in most cases is extremely slow. At the cedar swamp in Charlton, Mass., a tree about 35 feet in height and a foot in diameter showed 148 rings. The chestnut was a rapidly growing, but comparatively short-lived tree.[14] The largest stump which I found in southern New England, although 75 inches in diameter a foot from the ground, showed only 250 rings.

PRESENT DAY TENDENCIES

As the white pine-hemlock was the most striking and spectacular type in southern New England, it is deplorable that old stands could not have been preserved here and there. It would seem advisable to foster this type on reservations, estates, and in state forests, particularly in the white pine region. Although reproduction of white pine is abundant here, the high value of this tree for lumber leads to cutting it as soon as merchantable size is reached. There are many sites, however, even now where young white pines 50 to 80 years of age are associated with hemlocks and other trees in a proportion similar to the old groves, and if some of these could be saved and natural conditions preserved for a century or two, some of the aged and impressive appearance of the climax forest could be attained.

The value of the white pine is leading more and more to its culture in the white pine region. Fields and pastures are allowed to seed in. Attempts are made by owners to increase their acreage of pine. The value of hardwood groves lies in their fuel production, and when cuttings are made for this purpose, the scattered pines are usually spared with a view to their increase. Many sites are known which have been transformed from pine-hardwood to predominately pine in the past 15 years by simply removing the hardwoods

[12] In 1929 recorded as 24 feet 3 inches in circumference at the base and over 100 feet high.

[13] Spaulding (1899) records (p. 27) a white pine in Michigan, 48 inches in diameter breast high, 170 feet in height and 460 years old.

[14] Chestnut is frequently struck by lightning and many of the large old trees of 25 years ago showed the effect of lightning strokes. Probably the death of many of the larger older trees was hastened by this cause.

for fuel. There has been considerable planting of white pine with many thrifty young stands resulting, although some of these outside the white pine region have not been preëminently successful. The hazard of fire so destructive to young white pine is an ever-present menace to the white pine. During the past 25 years there has been a definite movement towards the protection of woodlands for aesthetic purposes, in the increase of state forests, state parks, reservations and estates.

Chestnut groves were fostered until the blight destroyed the species. The place of the chestnut in the forest is now being taken by other trees, principally oaks.

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THE LIFE OF FLATHEAD LAKE, MONTANA

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* Resigned 1934.

Contents

THE LIFE OF FLATHEAD LAKE, MONTANA

INTRODUCTION

In the summer of 1928 the Montana State Fish and Game Commission undertook an investigation of Flathead Lake to determine means of increasing its production of food and game fish, especially the eastern, or Lake Superior whitefish, *Clupea clupeaformis*, several plantings of which had produced only meagre results. The work was placed in charge of the biological staff of the University of Montana at Missoula, assisted by the departments of Physics, Chemistry and Geology. Active work was prosecuted from 1928 to 1932, the results of which are presented in the following paper.

I wish to express here our indebtedness to the Commission for their interest and financial assistance, to former Chancellor M. A. Brannon, President C. H. Clapp and Dr. M. J. Elrod for their cordial support of the project, while to my colleagues, Drs. G. D. Shallenberger and J. W. Howard, I am obligated for many of the data on the physics and chemistry of the lake. The U. S. Bureau of Fisheries aided us materially by the loan of equipment. For the botanical data I am indebted to my former colleague, Dr. J. E. Kirkwood, whose death in 1928 was a serious blow to our work; and to Dr. C. W. Waters, who succeeded Dr. Kirkwood in 1929.

For assistance in identification of material I am indebted to the following: Prof. Bert Cunningham, Protozoa; Dr. G. B. Twitchell, sponges and Bryozoa; Dr. Libbie H. Hyman, planarians; Mr. F. J. Meyers, rotifers; Mr. Gerald Thorne, nematodes; the late Dr. C. Dwight Marsh, copepods; Prof. Paul Welch, annelids; Dr. J. P. Moore, leeches; Dr. R. E. Coker, canthocamptids; Dr. E. A. Birge, cladocerans; Dr. W. L. Tressler, ostracods; Dr. J. G. Needham, Dr. O. A. Johannsen, Prof. H. B. Hungerford and the staff of the U. S. Nat. Museum, insects; Dr. Ruth Marshall, water mites; Dr. Junius Henderson and the late Dr. V. Sterki, molluscs; and Prof. C. J. Elmore, diatoms.

The plancton counts were made by Miss Elizabeth Barto, and most of the graphs by Mr. Russell Watson.

Previous Work

Many of the European lakes have been thoroughly studied hitherto and there are several studies on those of North America, but no thorough work has yet been done on any of the mountain lakes in this country, although preliminary investigations have been made on several.

Especial interest attaches to a study of Flathead Lake by the previous observations of Forbes (1893), rendering some comparison possible between present and past conditions; and more especially, by the probable construction of a dam below the outlet of the lake, which will, if completed, raise its

level by several feet and undoubtedly alter materially the present environment.

What are the present physical, chemical and biological conditions in Flathead Lake are questions which this paper will attempt to answer, as a basis of comparison for studies which may be made in the future when present conditions have been changed.

STATIONS

In the study of the lake, ten stations, which are shown on the accompanying map, were selected to represent, as nearly as possible, all of the different environments in the lake. Stations 2, 3 and 8 were in water averaging less than 3 m. in depth, while the others were at varying depths, down to 90 m. (No. 1). The environment at No. 4, just inside the mouth of the Flathead River, is very different from that in the open lake. The temperature averages about 3°C lower than at corresponding levels in the adjoining lake and the river carries a considerable load of sand and silt, which is being deposited in an extensive sand bar at its mouth.

Station 5 in a chain of islands cutting off Polson Bay from the main lake, is in a passage 100 m. wide and about 15 m. deep at low water, through which flows a large part of the water in the lake. This is the only point at which a current, due solely to the flow of the lake, has been detected.[1]

Observations were made at each station approximately twice a month during July, August and September 1928, and once a month from June to September in 1929. Additional collections were made at some of these stations at irregular intervals. At one of the stations (No. 1), selected to represent as nearly as possible the lake as a whole, observations were made at 6 to 14 day intervals from July 5 to November 3, 1928. In 1929 one series of observations was made in February, while from April 16 they were made bi-weekly or oftener until November 28, with exception of the intervals from July 12 to 31, August 9 to 30 and November 9 to 28. Thereafter one series was made on December 19 and 20 and one on February 3, 1930, when the plancton collections were ended.

In September 1930, and March to September 1932 several series of bottom samples for quantitative study were taken in Yellow Bay and the adjacent lake to determine depth distribution of the benthos. Besides these collections a large number of samples for qualitative study were made at many places in the lake, representing all possible habitats therein, and a few samples for quantitative study were made at points other than those enumerated above.

TOPOGRAPHY AND GEOLOGY[2]

Flathead Lake is 43 km. long and 24 km. wide. Its principal tributary is Flathead River which is formed by the union of three large forks about 50 km.

[1] See page 107.

[2] The data on geology and topography of Flathead Lake have been taken from a ms. report by President C. H. Clapp.

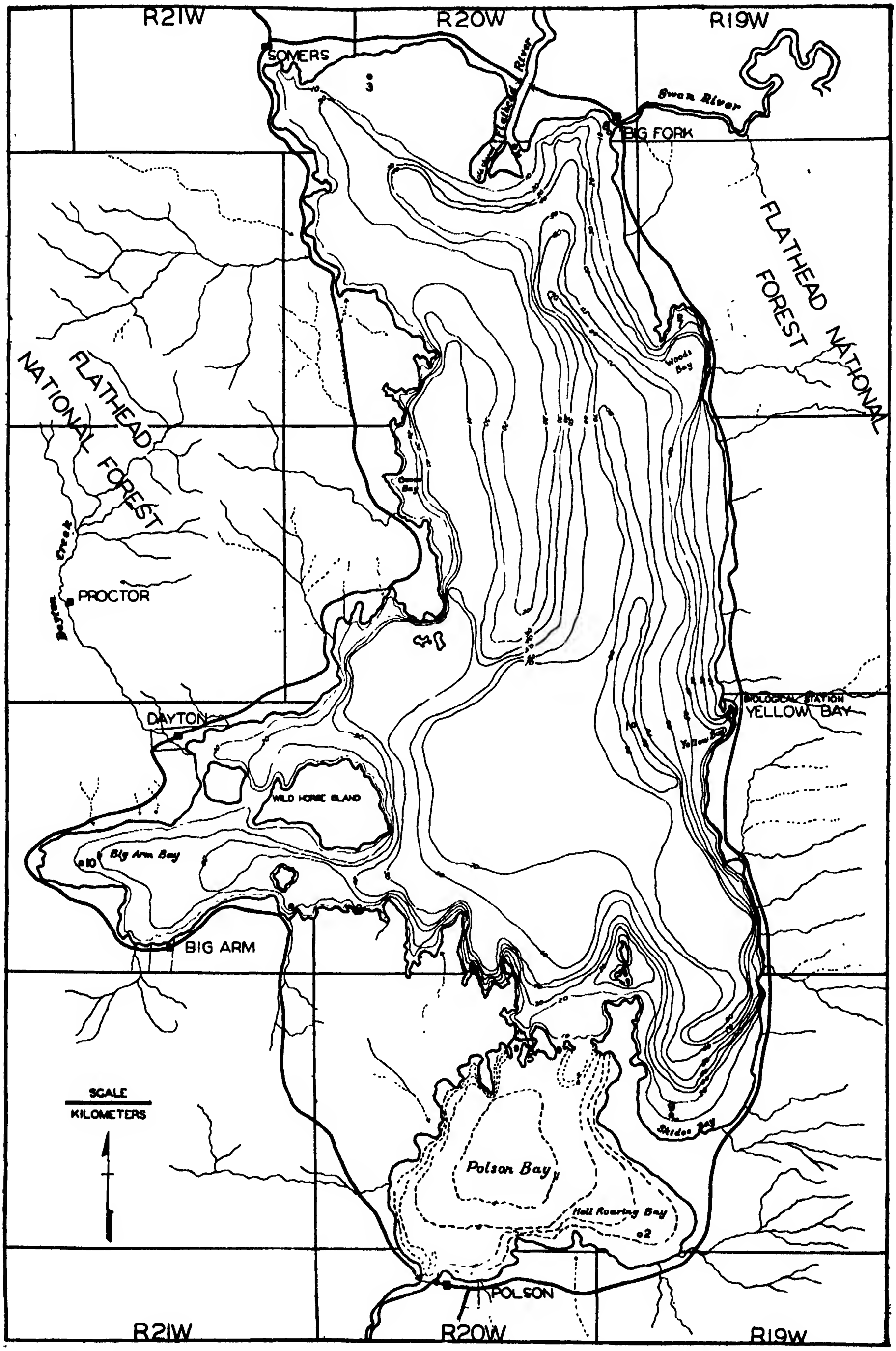

FIG. 1. Map of Flathead Lake from Graham and Young (1934) Depths in Meters. Locations of the Collecting Stations (1-10) indicated by circles.

northeast of the lake. Formerly the river entered the lake a little west of its present mouth, but as a result of meandering the old channel has been abandoned and now remains as a pool, or series of pools connected with the lake at high water only.

The lake is also drained by the Flathead River which flows swiftly through a tortuous channel with many rapids and falls to enter the Clark's Fork of the Columbia near Paradise.

Flathead Valley, which has a due north and south trend, is approximately 130 km. long and 10 to 30 km. wide. The lake fills almost the entire valley width, the mountains rising abruptly from the surface of the water at many points.

On the west side of the valley the mountains are lower, more rounded, and more extensively and deeply dissected by valleys than on the east side; where they rise sharply to form one of the most conspicuous and spectacular escarpments or mountain walls in the United States.

The accompanying map (Fig. 1) from the U. S. Land Office shows the general topography of the lake and its depths, which were located approximately by compass readings on prominent points of the lake shore, or in the case of those close to shore, by means of a measured line run from a boat to the shore. None of the locations pretend to be very accurate, but were the best that we could do with the time and means at our disposal, and give a sufficiently good idea of the lake contours. On a map of this scale (1:270,000) a variation of even 100 m. is inappreciable. As shown by the map the deepest portion of Flathead Lake is a rather narrow channel about 24 km. long and 4 km. wide, near the east shore, an arm of which extends westward to the mouth of Big Arm Bay.

The main body of the lake is from 30 to 75 m. deep, but the north and south ends are relatively shallow, having been partly filled with sediment. Its greatest depth is about 100 m. varying of course with the water level.

During the Glacial Age, Flathead Valley was nearly filled with a huge valley glacier, fed from the north and from mountain glaciers on the east and perhaps on the west as well. The valley was filled to a height of about 800 m. above the present lake level and rocky ledges below that elevation have been smoothed and rounded by glacial scour. On the retreat of the glaciers Flathead Valley and the larger tributary valleys were partly filled with glacial drift and sands and silt deposited by streams from the melting glaciers, which built a terminal moraine 138 m. high at the foot of the present lake, and through which the present river has cut its way to bed rock.

The length of the shore line, not including the islands, is approximately 185 km. about 55 km. of which are mud or sand, 50 of rocky and pebbly beach in the bays, and the remainder rocky cliffs. The rocks of the shore are quartzites, argillites and limestones. The erosion of the latter, which is more uneven than that of the others, has resulted in the formation of numer-

ous little headlands, and small islands, especially near the southern end of the lake.

The area of the basin drained through Flathead Lake, chiefly by Flathead River and its three forks, is 18,000 sq. km. The amount of water flowing annually through the lake varies from 80 to 120,000,000 cu. m., averaging about 100,000,000 cu. m.

Since 1907 the U. S. Geological Survey has maintained river gauges on the principal tributaries and the outlet of Flathead Lake. From 1907 to 1925 the maximum discharge was 2325 cu. m. per second on June 13, 1913 and the minimum 38. 5 cu. m. per second on March 14, 1920, while the rise and fall of the lake from 1908 to 1928 ranged from a maximum of 4.27 in 1913 to a minimum of 1.49 m. in 1915.[3] High water usually occurs in May or June and low water in February or March.

The supply of the lake comes chiefly from the numerous alpine lakes at the sources of the Flathead and Swan rivers, many of which are fed by the glaciers and snow banks of Glacier Park, an area of high and rugged mountains about 80 km. northeast of the lake.

Most of the surrounding region is wooded, but portions of the drift covered plain of the upper and lower valley and around Big Arm has been cleared, or are treeless. Some of the steeper neighboring slopes have been cleared for a short distance from the lake for fruit and vegetable farms.

BOTTOM DEPOSITS

Around much of the lake large rocks extend for varying distances from shore, being succeeded by gravel of gradually diminishing size, and this in turn by the almost impalpable ooze, which covers most of the lake bottom. In general the rocks and gravel extend to a depth of about 30 m. but this depth is of course very variable. In certain places, i.e. at the north and south ends of the lake and to a less extent elsewhere, the rock and gravel bottom is replaced by sand, or the ooze may extend to the shore, while the floor of the bays may be covered to a considerable extent by sunken logs and woody fragments.

The ooze, which covers so much of the lake floor, is composed of fine particles of sand, clay and organic detritus ranging in size from 10 to less than 1μ. Diatoms, both living and dead, are common, especially in the bays, together with pollen and various plant fragments of an indeterminate nature. Its color varies from point to point, dependent on the character of the adjacent shores and the method of its deposition, ranging from blue gray or brownish to a dirty yellow. In some places the color may change rather abruptly in the same area and in different layers, but to what extent minor currents may be responsible for this is unknown.

No chemical analyses of the ooze have been made, but no H_2S has been

[3] Elrod (1901) reports a rise of 5.8m. in one season.

found in the bottom water, while increase of CO_2 and decrease of O_2 near the bottom are not pronounced; so it is evident that decay is not active here. This is to be expected, from the low temperature and the scarcity of bacteria in the lower levels of the lake, as described by Graham and Young (1934).

CLIMATE

Flathead Lake lies in a region of low rainfall and moderate temperature. Records of the U. S. Weather Bureau (to 1933) at Kalispell, 16 km. north of the lake, show a mean annual temperature of 6.0°C for a period of 34 years, while at Polson, on the southern shore of the lake, the mean annual temperature for a period of 20 years was 7.2°. Absolute maximum and minimum at Kalispell are 37.2° and —36.7°, and at Polson, 40° and —31.1° respectively.

The average annual rainfall at Kalispell is 37 cm. and at Polson 39 cm., with a maximum and minimum of 49 and 26 cm. at Kalispell and 53 and 26 at Polson respectively, while the average number of sunny days (at least 75% sunshine) is 97 at Kalispell and 149 at Polson.

The average annual snowfall at Kalispell is 111 cm., the heaviest average monthly fall being 27.5 cm. in January and the lightest a trace in July with absence of snow in August only. At Polson the average is 113 cm. with a maximum average of 32 cm. in January, and none in May, July and August.

Total wind movement at Kalispell for 32 years was 67277 km. per year, with a maximum velocity of 64 km. per hour. The windiest months are April, May and June. There are no data on wind movement at Polson.

Prevailing wind directions are northwest at Kalispell and southwest at Polson. Apparently the slightly higher temperature over the lake than in the surrounding region creates an upward draft, causing wind drift from both north and south, with a rising air current over the lake and counter currents at higher levels. Since there are no data for wind movement at various points on the lake and at higher levels in the mountains it is impossible to test this hypothesis.

PHYSICS—LIGHT

The penetration of light in lakes is measured in various ways. The simplest and most generally used method is that of the Secchi disk, which is relative only and involves a personal factor.

Another method depends upon the use of photographic plates or films. Such a method is open to the objection that different emulsions have different sensitivities, not only in degree (speed) but also in quality (with reference to the spectrum). It is further subject to the limitation that in comparing any two intensities of light it is necessary that the densities and times of exposure be the same.[4] Therefore it is necessary to compare the intensities

[4] See Klugh (1925).

by means of screens of known transmissions placed over the sensitive plate or film. Such a method involves considerable technical difficulty and expense, and has not, as yet, come into general use, although several workers have recently employed it.[5] In a third method certain chemical substances, such as uranyl oxalate, enclosed in tubes of glass or quartz, are exposed to light at various depths and the rate of decomposition noted. This method has recently been used by Atkins and Poole (1930) in comparison with the photo-electric, or fourth method, to be described below. These authors found that with glass tubes the average ratio between the absorption coefficients, photo-chemically determined, and those determined by the photo-electric cell was 1.1 :1.0.

A fourth method involves the use of various electrical devices. Regnard (1891) used a selenium cell and galvanometer for this purpose, the resistance of the selenium varying with the intensity of the light. Birge and Juday (1930), in their work on the Wisconsin lakes and elsewhere, have employed the pyrlimnometer, which measures the heat effect of light by means of a thermopile; while Shelford and his colleagues,[6] and Poole and Atkins (1925) etc. have used the photo-electric cell.

The sensitivity of this cell varies with the kind of metal employed, whether the latter is mounted in gas or vacuo, on the kind of glass in the window of the cell, on the diameter of the latter, and on many other conditions, the details of which cannot be given here. The cell furthermore is relatively insensitive to red light.

In our own work on Flathead Lake we have employed the Secchi disk, photographic plates and filters and the Kunz photo-electric cell described by Shelford and Gail (*l.c.*). The latter has been adapted to our purpose and operated by Dr. G. D. Schallenberger of the Dept. of Physics of the University.

In operating the Kunz cell in 1928 and 1929, Dr. Shallenberger employed a 10 m. launch which was sufficiently stable on quiet days for this purpose. Due to difficulties of construction and operation—the latter depending on conditions of wind and sky—but few satisfactory sets of determinations have been made with this instrument, three of which are shown in Table 1 and Fig. 2.

A comparison of these results with those of Shelford and Gail (*l.c.*) on Puget Sound, shows a rather close agreement down to the 10 m. level, but below this they diverge widely. At 50 m. the latter found an illumination of 1,388 m.c.[7] or about 1.5% of 93,100 m.c.[8] in air, while the former's results show only 7.8 m.c.[9] at 50m., or .01% of the 72,600 m.c.[9] reading in air on the same dates. I can only surmise the reason for this difference since I

[5] Klugh (l.c. and 1927), Lönnerblad, (1929), and Oberdorfer (1929).
[6] Shelford and Gail (1922), and Shelford and Kunz (1926).
[7] Mean of 5 readings.
[8] Mean of 16 readings.
[9] Mean of 4 readings.

have insufficient data for Puget Sound water to compare with our own data for Flathead Lake. Probably the difference is due to larger quantities of plancton in the latter, but of this I have no information. Whipple (1927) gives the limit of visibility of the Secchi disk as 59 m. in the "Pacific Ocean", but for a body of water of that size such data are rather indefinite, and whether they apply to Puget Sound or not is not known. It is evident, however, from all the data available that sea water is in general much clearer than fresh

TABLE 1

LIGHT PENETRATION IN METER CANDLES AT STATION 1 ON THE DATES AND AT THE TIMES RECORDED.

Sun = reading in air.
Water = reading in water at the given depth. The 0 reading is with the cell just below the surface.
Ratio = the fraction of light transmitted by each 3 m. layer.

Observation No. 1. August 20, 1928.

Depth	Time	Sun	Water	Ratio
0	9:52	45,800	34,000	.72
3	9:53	46,100	14,600	.43
6	9:54	46,100	6,170	.42
9	9:54	46,100	3,900	.63
12	9:56	46,100	2,100	.54
15	9:57	47,200	1,240	.59
18	9:58	47,200	775	.62
21	9:59	47,700	325	.42
24	10:00	47,700	207	.64
27	10:01	47,700	128	.63
31	10:02	47,700	68.7	.54
34	10:03	47,700	41.5	.60

TABLE 1

Observation No. 2. July 23, 1929.

Depth	Time	Sun	Water	Ratio
0	11:50	66,500	48,000	.73
3	11:52	66,500	22,000	.46
6	11:53	66,500	10,500	.48
9	11:54	66,500	6,500	.62
12	11:55	66,500	3,700	.57
15	11:55	66,500	2,400	.65
18	11:56	66,500	1,390	.58
21	11:57	66,500	765	.55
24	11:58	66,500	450	.59
27	12:00	66,500	265	.59
31	12:00	66,500	160	.60
34	12:01	67,500	92	.58
37	12:02	67,500	57	.62
40	12:03	67,500	36	.63
43	12:04	67,500	22	.61
46	12:05	67,500	13	.59
49	12:06	67,500	8	.62
52	12:07	67,500	4.5	.56
55	12:09	67,500	3.0	.67
85 calc.	.....	......	.016248	...

TABLE 1
Observation No. 3. July 25, 1929.

Depth	Time	Sun	Water	Ratio
0	12:35	77,500	59,000	.76
3	12:33	77,500	29,000	.49
6	12:32	77,500	13,500	.46
9	12:32	77,500	8,100	.60
12	12:31	77,500	4,900	.60
15	12:31	77,500	3,000	.61
18	12:30	77,000	1,840	.61
21	12:30	77,000	1,000	.54
24	12:29	77,000	626	.63
27	12:28	77,000	397	.63
31	12:28	77,000	225	.57
34	12:27	77,500	140	.62
37	12:27	77,500	85	.61
40	12:26	77,500	55	.64
43	12:25	77,500	35	.64
46	12:25	77,500	20	.57
49	12:24	77,000	12	.60
52	12:23	77,000	7	.58
55	12:21	77,000	5	.71
58	12:20	77,000	3	.60
85 calc.	.....	......	.0228	...

water, which probably explains the difference in Shelford's and Shallenberger's results.

Poole and Atkins (1925, '26, '29 and '31) using photo-electric cells of various types obtained readings down to 70 m. in the English Channel. Their results average considerably higher than those of Shallenberger at depths of 50 m. and more, but on September 7, 1927 they record a transmission at 50 m. of only .0055%, which is somewhat less than the latter's results for Flathead Lake. The lowest illumination they record is 2.5 m.c. at 60 m. on the same date, while the lowest reading obtained in Flathead Lake was 3 m.c. at 58 m. on July 25, 1929. At 70 m. these authors found a transmission of 0.121% on May 7, 1928, while in Puget Sound Shelford and Gail (*l.c.*) record a reading of .01636% at 200 m.

Poole and Atkins (1928) have attempted to correlate Secchi disk readings with those obtained by means of the photo-electric cell, from which they conclude "that both the absolute and the percentage values of the illumination at which the disk was just visible varied widely. This was probably due to variations in the surface which would probably have a greater effect on the visibility of the disk than on the illumination." (*l.c.* p. 481). Their tables, however, show clearly that *in general* there *is* a positive correlation between visibility of the Secchi disk and transmission of light as measured by the photo-electric cell, as might be expected.

Oberdorfer (1929) employing a filter-wedge photometer gives a maximum transmission of 0.96% in March and a minimum of 0.11% in September

at 25 m. for Lake Constance. The maximum depth of visibility of the Secchi disk in this lake is given by Auerbach et al. (1924) as 16.7 m. in February.

Klugh (1927) with a similar type of apparatus found a penetration of 10% at 10m. in the Chamcook Lake, a clear water lake in New Brunswick, and 70% at 0.5 m.

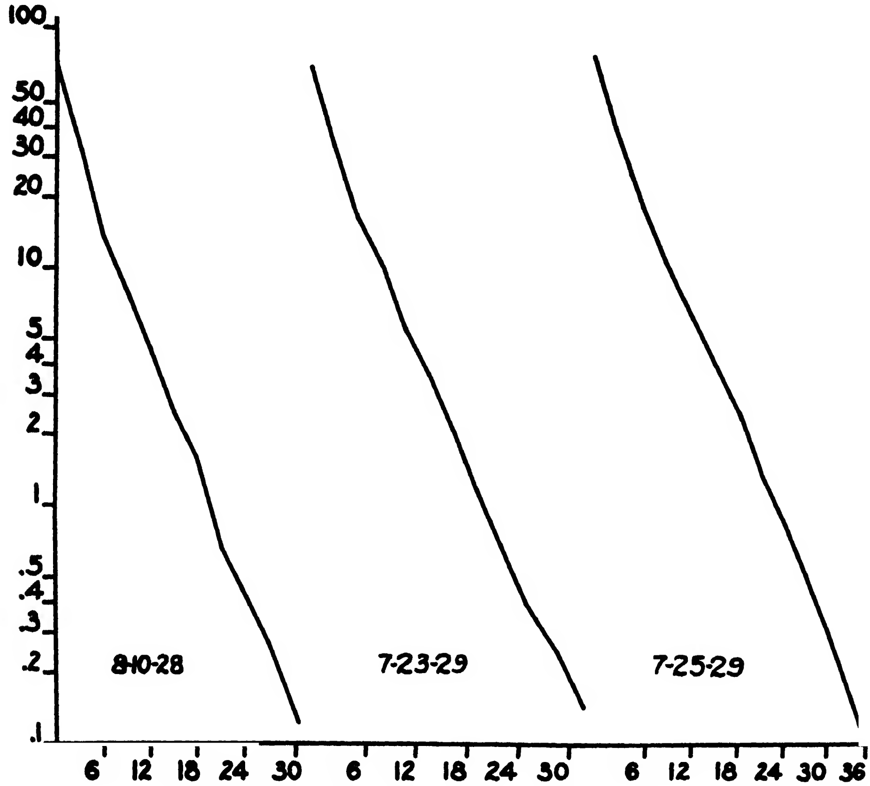

FIG. 2. Graphs showing penetration of light in Flathead Lake, plotted to a semi-logarythmic scale. Depths are given as abscissae, percent of penetration as ordinates.

In Lake Mendota, Shelford and Kunz (1926) find a transmission of only 0.23% at 10 m.,[10] a result undoubtedly due to the large amount of plancton in this water; while Lönnerblad (1929) finds that in certain lakes of the Aneboda district in Sweden light penetration reaches a depth of only 6-7 m., a result which is doubtless due to the high color of these lakes from dissolved humus materials.

In general the results show a much higher penetration for Puget Sound waters than for the English Channel; or for inland waters generally. It is evident, both from these results, and from the Secchi disk readings above

[10] Computed from Table 1 in Shelford and Kunz (*l.c.*).

cited, that the former water is far more transparent than the other waters so far studied. An examination of clear deep lakes like Crater or Tahoe would be of much interest for comparison.

A glance at Table 1 will show that considerable variations exist in the percentages of light transmitted by different layers,[11] a result strictly in agreement with those of Shelford and others, and which is perhaps attributable to irregularities in vertical distribution of the plancton.

While it was impossible to obtain results with the photo-electric cell below 58 m., on the basis of results down to that point the calculated result for 85 m., the level at which most of our bottom plancton samples were taken, gives an estimated transmission of only .01818 m.c. or .000025%. As an approximate check on this result, I have made a comparison of the amount of light at 0:6 m. and at 85 m. by means of Cramer's "Spectrum process" plates covered with screens of varying densities, whose transmission percentages were determined in the Physics Laboratory of the University of Montana; the result of which, on October 18, 1931, gave a transmission at the lower level of .00007% of the light present at the higher level.

Assuming a transmission of 67% at 0.6 m., which is estimated from the results of Shelford and Gail, Poole and Atkins and Klugh and from those of Shallenberger on Flathead Lake, we should have a total transmission of .00007% x 67% or .000047% at 85 m. on this date; which result agrees fairly well with that of Shallenberger, considering that the former was determined in the autumn, when the water is much clearer than in July, when the latter was obtained.

A few determinations of light transmission in Flathead Lake have been made with the Secchi disk, a maximum reading of 13.2 m. being obtained on September 26, 1931, and a minimum of 4.5 m. on June 21, 1932. Under the ice in mid-winter I obtained a reading of 12.2 m. on February 3, 1930. The results are given in Table 2 which shows higher visibility in winter than in summer, a result which accords with those of other investigators, and is probably due primarily to the sediment which is deposited in the lake from the melting snows in spring and early summer and secondarily to the plancton maximum of this season.

TABLE 2. Visibility at different seasons in terms of depth of disappearance of a white disk (20 cm.) in diameter.

Date	Depth	Remarks
2/ 3/30	12.2 m.	Partly overcast sky, ice 15 cm. thick.
5/15/32	9.4 m.	Clear.
6/21/32	4.5 m.	Clear.
7/21/32	7.0 m.	Clear.
8/16/32	11.1 m.	Clear.
9/26/31	13.2 m.	Clear, but hazy.

[11] From 65.5% for the bottom to 46% for the upper 3m.

Judged on the basis of Secchi disk readings, Flathead Lake shows a penetrability intermediate between turbid lakes like Mendota and transparent lakes like Tahoe.[12]

As may be seen from the above brief summary of the work on the penetration of light in various waters, the problem is full of difficulties and the results are widely variable. Some of the difficulties involved are, first, those of a mechanical nature, such as obtaining a boat which is sufficiently steady for the use of delicate instruments (galvanometers), and water-proofing the electrical apparatus for work at great depths. Second, changes in the amount of light from the sky from moment to moment; variations which may not be visible to the eye, but which are nevertheless easily detected by delicate instruments. When clouds are passing across the sun the light intensity may vary from moment to moment by 100% or more. Thus in series 28 of Poole and Atkins (1929) the light in air varied from 73500 m.c. at 3.53 p.m. (4-19-28) to 25300 m.c. at 3.58 p.m. with the passage of a cloud. Third, changes in water surface may vary the light intensity by similarly great amounts, Shelford and Gail (*l.c.* p. 161) noting a variation from 67.3% to 26.0% in three minutes. A fourth difficulty, and one which is present in photometry in both air and water, is presented by the light angle and by the amount of reflection from glass surfaces. The effect of obliquity may be reduced or eliminated by the use of suitable diffusing glass windows (Poole and Atkins, 1929), but such windows absorb considerable amounts of light and thereby reduce the sensitivity of the apparatus.

We have little knowledge of the relative values of the direct and reflected light in water, but Poole and Atkins (1931) have found values of 0.22 to 0.61 for the ratio of the horizontal to the vertical light at depths between 0 and 30 m.

In relation to the biological significance of light in water, two considerations must be borne in mind. First, the total illumination, both in kind and intensity, is the factor which is effective in determining the growth, and therefore, abundance of photo-synthetic organisms; while, second, the direction of the light, in addition to its quality and intensity, is effective in determining the movement, and therefore distribution of phototropic types.

None of the data obtained thus far throw adequate light on either of these questions. They serve merely as a beginning in elucidating a most difficult, but interesting problem. They indicate, however, the extremely small quantities of light under which many organisms may live and enjoy active growth and reproduction.

The recent work of Hentschel (1928) and Schiller (1931) is of much interest in this connection. They found olive-green cells of uncertain relationship (Chroococcales or Chlorobocteriaceae?) at depths of 1200 m. in the

[12] Mendota, 1.75m. (Birge and Juday, 1911), Tahoe 33m. (Whipple, 1927).

Adriatic (Schiller) and even at 4000 m. in the Atlantic (Hentschel). Schiller is probably correct in his assumption that these cells may live in total darkness, for the maximum penetration of light which I have found recorded, is 1500 m., by Grein (1913).

Several turbidity tests have been made with the Jackson turbidimeter,[13] both in the open lake, the shallow bays and the mouth of the Flathead River, a maximum reading of 165 being obtained in the latter on May 14, 1932 when the river was in flood. No other reading has approached 25, the lowest recorded by this instrument. Heavy gales may, however, stir up the bottom of the shallow bays, rendering the water very turbid, but I have never made a reading at this time. A large amount of sand and silt is carried down by the Flathead River, and deposited on a sand bar, which extends many hundred metres from its mouth.

Early in 1916, a year of exceptionally high water, Dr. M. J. Elrod noted areas of very turbid water. In MS. notes he says "the blue, clear water usually ended abruptly at different places, changing to water of a dirty yellow into which (one) could see but a few inches." Similar conditions were observed on May 14, 1932 when there were numerous patches of very muddy water interspersed with clearer ones, extending some distance beyond the mouth of the Flathead River.

The color of the lake water is very faintly blue. The Flathead River, at least in early summer, is slightly brownish, giving a color value of between 10 and 15 p.p.m. on the platinum-cobalt scale of the American Public Health Association,[14] but we have never been able to get any readings on this scale in the lake itself. There is only a single reading, taken in Yellow Bay, in late summer or early fall of 1931, with Forel's standard.[15] This reading showed no sign of yellow in the water, for it failed to match a dilution of 5 ppm. of potassium chromate. Compared with an ammoniacal solution of copper sulphate, however, it matched a dilution of 25 ppm.

TEMPERATURE

The temperature cycle in Flathead Lake is similar to that in deep lakes elsewhere in the temperate zone, those having a well defined thermocline with a wide range of temperature at the surface and a small range at the bottom.

It is seldom that the lake freezes, except in the shallow bays, three exceptional years being 1929, 1930 and 1933. Our records include only the winters of 1929 and 1930 when the lake froze, but it is safe to assume that the winter temperature always reaches at least 4°C. at which point the period of winter stagnation occurs.

With the warming of the surface in spring an upper layer of warmer water, the epilimnion, gradually appears, separated from a lower, colder layer

[13] Whipple and Jackson (1900).
[14] Standard Methods of Water Analysis.
[15] Steuer (1910, p. 47).

by a well marked thermocline. The latter first appeared in 1929 shortly before May 18, or about a month after the ice left the lake.

From this time on the rapidly rising air temperature raises the temperature of the surface layer of the lake and the thermocline gradually descends, reaching a depth of about 30 m. by the middle of October and about 45 m. by the end of November. The rate of descent is not constant but varies apparently with the wind. The relation between the thermocline and the wind has not been adequately studied, however.

As the thermocline descends and the epilimnion gradually cools in the lowering temperature of autumn, the former slowly fades out, until, with the approach of winter, it entirely disappears and the circulation of top and bottom water is complete, with the temperature uniform from top to bottom. This condition was present on December 20, 1929 and probably for several days prior thereto.

There now ensues a period of inverse stratification, but without the establishment of a definite thermocline, due to the lowering temperature of winter cooling the surface water below 4°, the point of maximum density, while the lower layers are gradually and incompletely losing their heat by conduction.

TABLE 3. Variation of temperature with depth and time on September 9, 1928.

Time	Depth	Temperature	Wind and Sky
9:15 A.M.	0.0	15.3	Moderate north breeze, light sun.
9:20	1.5	15.4	
9:30	3.0	15.4	
9:40	4.5	15.4	Light cloud.
9:45	6.1	15.4	
9:55	9.1	15.3	
10:05	10.6	15.2	
10:20	12.2	15.15	
10:35	13.7	14.9	
10:40	15.2	14.2	
10:50	16.7	13.5	
11:00	18.3	12.5	
11:10	19.8	12.0	
11:20	21.3	10.8	
11:25	22.8	9.9	Light Sun
11:40	24.4	8.15	Part cloud.
11:50	25.9	7.6	
12:00 P.M.	27.4	8.1	
12:10	27.4	8.3	
12:15	27.4	8.4	
12:25	27.4	8.4	Fresh south wind, increasing in strength.
12:35	25.9	9.0	Rough sea.
12:45	30.5	8.0	
12:55	24.4	10.2	
1:05	60.9	5.6	
1:10	22.8	10.8	
2:10	94.0	4.6	
2:20	21.3	12.25	
3:50	0	15.4	High southwest wind.

Due to the changes briefly outlined above the surface temperature of Flathead Lake has an annual range of about 20° C. while that of the bottom (90 m.) is less than 3°. These relations are shown in figures 3, 3a and 6-9. The zigzag form of the curves, which is much more pronounced in the upper 30 m. than it is below 60 m. is evidence of the influence of the wind in creating currents in the lake, either directly, or by convection. The profound influence of wind on the distribution of temperature in a lake is beautifully shown in Fig. 50 in Whipple (*l.c.*), taken from observations by Watson on Loch Ness, Scotland, and has been discussed in detail by Kühl (1928) for the Walchensee in the Bavarian Alps. The inconstancy of temperature and the rapidity with which changes may occur are well shown in Kühl's Table 2, (*l.c.* p. 63) and in our own Table 3.

CURRENTS

Measurements of lake currents were made by Dr. Shallenberger with an instrument of his own device. He has supplied the following data.

While the general movement of the lake is necessarily from north to south it has not been possible to detect any current produced thereby except at Station 5, in the narrow channel between the islands at the entrance to Polson Bay at the southern end of the lake. The only currents found in the main body of the lake are those due undoubtedly to wind. In these there was considerable variation in direction and magnitude. On one occasion, following several days during which a strong wind blew from the south, a northward current was observed at station No. 1. This current had a value of 1200 m. per hour at the surface, and of 50 m. per hour at a depth of 15 m. Even at Station 5, where the main body of the lake flows through a channel about 100 m. wide and 15 m. deep, and where in calm weather the surface current is about 800 m. per hour southward, a northward current of 540 m. per hour may be caused by a strong south wind.

Table 4 shows how the current at Station 5 varied with depth on a calm day. Observations were made on August 10, 1929 on a southwardly directed current.

Table 5 shows how a northwardly directed current varied with depth on July 8, 1929, at Station 1.

Unfortunately there are no data on the thermocline for July 8, when the readings at Station 1 were taken. On July 12 it lay between 7.5 and 11 m. and was probably not much, if at all lower than this on July 8. Water movement must have extended therefore to a considerable depth below the thermocline, since the table shows it to have reached a depth of at least 15 m.

These results, obtained in summer, may not give even approximations of the maximum wind effect on currents throughout the year. They indicate in any case, however, the importance of wind in disturbing the surface layers

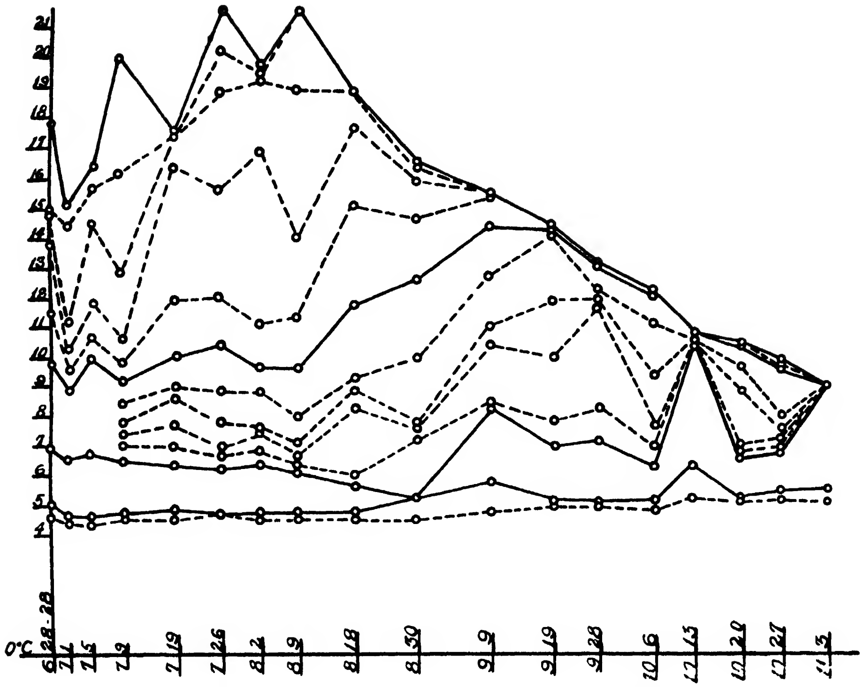

FIG. 3. Seasonal distribution of temperature. 1° C. = 1 division of the vertical scale. Temperatures at 0, 15, 31, and 61 m. are shown as full lines, while those at intervening depths are shown as broken lines. The bottom temperatures (85-91 m.) are shown as a single line. The slight variation between these depths is negligible.

of the lake down to a depth of at least 15 m., and thereby undoubtedly influencing the vertical distribution of temperature, gases and plancton in the lake. At the average rate of movement in the upper 2 m. of the lake on July 8, 1929 (Table 5) a mass of water would move the entire length of the lake in about 30 hours. Any movement of the surface layer in one direction necessarily involves a return movement at lower levels. Since a strong wind may blow uninterruptedly for several days, the entire surface layer of the lake may be turned over several times in the course of a single storm, and its temperature and chemical and biological contents be materially affected thereby. As these observations are very fragmentary, they give only a general conception of what actually occurs.

TABLE 4

Depth in m.	Current in m. per hr.
0	800
1	540
2	400
3	240
4.5	80

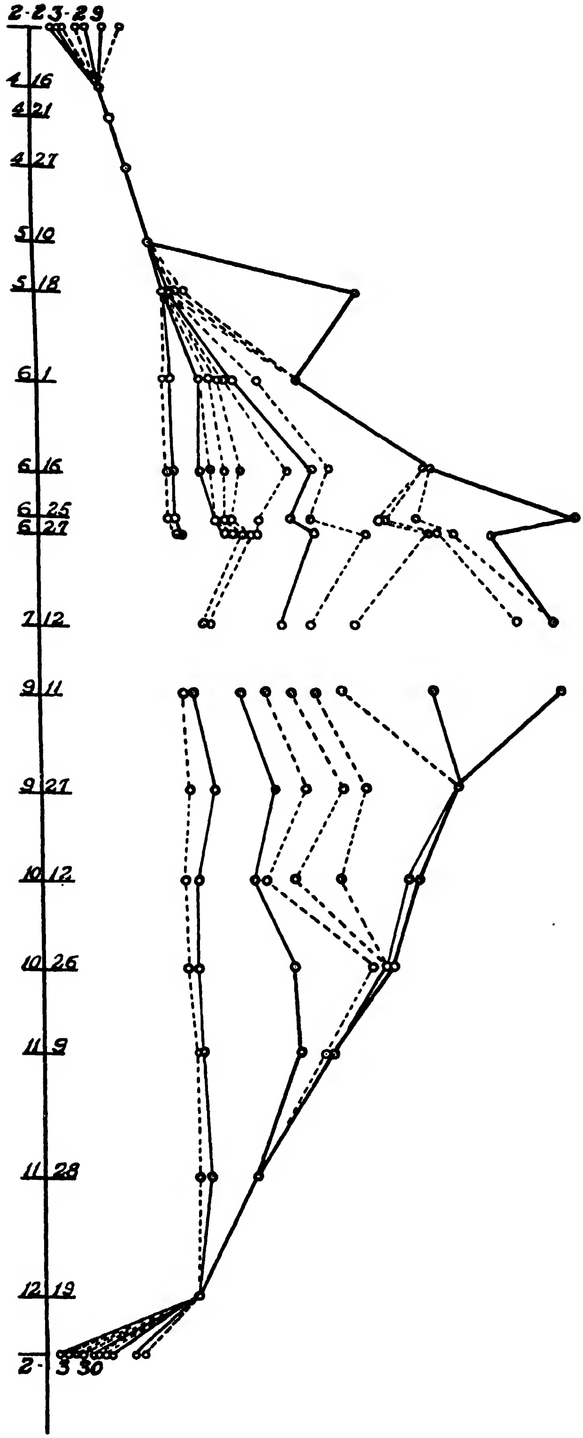

FIG. 3a

For description see Fig. 3.

A comparison of readings of the United States Geological Survey gauges at Somers and Polson show occasional differences in level of as much as 10 cm. at opposite ends of the lake. These differences may be due either to wind or inflow. They are, however, never large and probably exert a very minor influence on the life of the lake.

TABLE 5

Depth in m.	Current in km. per hr.
0	1.21
0.3	1.53
0.6	1.65
1.2	1.53
2.1	1.38
3.0	1.29
6.1	0.64
12.2	0.32
15.2	0.16

CHEMISTRY

Samples for chemical analysis were obtained with the Kemmerer water bottle (Kemmerer et al. 1923) until the loss of the latter, when a larger sampler designed by Dr. Shallenberger was substituted.

The chemical character of Flathead Lake is shown by the following analysis (Table 6) made by Dr. Howard. Samples for this analysis were taken at three widely separated points in the lake (Stations 1, 2 and 3). The results at all three points are practically identical. While this analysis indicates a water of high purity, it is not especially so, when compared with some other mountain lakes. Thus Lake Chelan in Washington, and Priest and Hayden lakes in Idaho have a total solid content which averages not much above 50% of that of Flathead Lake. On the other hand, when compared with other deep mountain lakes and with some European lakes, the total solid content is comparatively low. A comparison of twelve lakes is given in Table 7 which also shows their depths and the sources from which the data were obtained.

TABLE 6

Chemical analysis of Flathead Lake water in parts per million

Silicon Dioxide	8.2
Aluminum Oxide	9.38
Calcium Oxide	28.0
Magnesium Oxide	8.8
Chlorides	0.315
Nitrates	.0008
Sulfates	24.97
Sodium Oxide	0.865
Iron Oxide	0.016
Nitrites	0.000
Total solids	85.0

TABLE 7. Total solids of 12 lakes.

Location	Depth in meters	Total solids in parts pr. million.	Reference
MOUNTAIN LAKES			
Flathead, Montana	100	85	
Bear Lake, Idaho	55	1060	Kemmerer et al. (1923)
Hayden Lake, Idaho	58	52	"
Lake Pend Oreille, Idaho	366	146	"
Priest Lake, Idaho	113	49	"
Lake Chelan, Washington	454	44	"
Teleckoje Lake, Altai Mountains	325	56–60	Lepneva (1931)
Lake Geneva, Switzerland	310	171	Thienemann (1925)
Lake of Halstatt, Austria	409	158	Steuer (1910)
PLAINS LAKES			
Lake Mendota, Wisconsin	25	157	Birge and Juday (1911)
Lake of Plön, Germany	60	208	Thienemann (1925)
Greifen, Switzerland	32	190	Guyer (1911)

The nitrogen content of water is one of the limiting factors of its life, since nitrogen is an important element in the food of both animals and plants. A direct relation, however, between the productivity of a lake and the amount of nitrogen present cannot always be demonstrated. Thus, according to Domogalla et al. (1925) in Lake Mendota there is no relation between the variation in amount of phytoplancton and of nitrogen, while Utermöhl (1925) claims that in a small lake in Holstein nitrogen (and phosphorus) are not limiting factors in the development of phytoplancton. There can be no question, however, of the importance of nitrogen as a factor in the productivity of water, even though its immediate role be obscured by the multiplicity of other factors which govern this productivity. The relation of phosphorus in this connection is likewise problematical. While some authors (i.e. Seligo, 1926, Atkins, 1923, '25, '26, and Atkins and Harris, 1924) maintain its importance, others, i.e. Juday et. al. (1928) Minder (1926), and Tressler and Domogalla (1931) question this.

Nitrogen analyses were made at five widely separated points on the lake during the summer of 1928, and one at the mouth of the Flathead River in June 1929, when the river was in flood. The latter analysis was made to determine the amount of food material brought into the lake by the melting snows and rains of early summer. These analyses were made on the unfiltered water and hence do not differentiate between the dissolved nitrogen and that present in the form of plancton. Birge and Juday (1926) have shown that in Lake Mendota the ratio between the former and the latter is about 9:1. The results, which are rather brief and wholly inadequate for a study of seasonal variations in nitrogen, are given in Table 8. They indicate a greater amount of free NH_3 at lower levels than at the surface of the lake, which may be due either to loss of this gas at the surface through evaporation, to con-

sumption by plants, or to oxidation to nitrites and nitrates and the absorption of the latter by algae and Protozoa. The absence of nitrites and nitrates indicates that if ammonia is oxidized to these compounds, they are used up as fast as formed and hence do not appear in the analyses. Direct use of ammonia by chlorophyl-bearing organisms has been claimed by Pütter (1909).*

TABLE 8. Nitrogen analysis in parts per million.

Location	Date	Organic N.	Free NH_3	NO_2	NO_3
Station 1 (Main Lake), surface..............	7/5/28	0.1548	0.062	0.0	0.0
Station 1 (Main Lake), 31 m................	"	0.138	0.108	0.0	0.0
Station 1 (Main Lake), 92 m................	"	0.138	0.108	0.0	0.0
Station 2 (Hell-Roaring Bay), surface........	7/7/28	0.074	0.026	0.0	0.0
Station 5 (Narrows), surface................	"	0.090	0.038	0.0	0.0
Station 5 (Narrows), 15 m..................	"	0.132	0.048	0.0	0.0
Station 3 (Somers), surface.................	7/14/28	0.106	0.660	0.0	0.0
Station 4 (Mouth of Flathead River), surface .	"	0.026	0.018	0.0	0.0
Station 4 (Mouth of Flathead River), surface .	6/18/29	0.104	0.048	0.0	tr
Average..........................	......	.107	.131	0.0	tr

According to the work of Domogalla et al. (1925) on Wisconsin lakes the ammonia, nitrites and nitrates, which "originate in all probability from the decomposition of organic forms of nitrogen contained in the mud and debris at the bottom of the lake" (*l.c.* p. 278), are more abundant in the lower than the higher levels except at the time of the spring and fall turn-overs, when the distribution of dissolved substances becomes uniform from top to bottom. A similar distribution of nitrates in Lake Zürich is described by Minder (1926), who attributes this to their consumption by the more abundant phytoplancton near the surface.

These results do not agree with those of Burkholder on Lake Erie (Fish, et al., 1928) where free NH_3 is 2.5 times greater at the surface than the bottom in mid-summer. Burkholder attributes this to bacterial action, but in Flathead Lake Graham and Young (1934) found no evidence of denitrifying bacteria at the surface, although they were active at lower levels.

The relatively large amount (0.66 ppm.) of free ammonia at Station 3 (July 14, 1928), may have been due to the presence of a log jam in the neighborhood.

The results obtained at the mouth of the Flathead River on July 14, 1928 and June 18, 1929, which show much larger amounts of organic nitrogen and free ammonia on the latter date, suggest the effect of surface drainage on the nitrogen content of the river, due to higher water from rain and melting snow in the mountains.

* Since this ms. went to press I have learned of some experiments of Dr. C. E. Zobell of the Scripps Institution of Oceanography, which demonstrate the direct utilization of NH_3 by various marine organisms (Nitschia, Chlorella, etc.)

A comparison of the nitrogen content of Flathead Lake with that in some other lakes is given in Table 9, which shows also the depths of these lakes and the sources of information.

TABLE 9. Comparative nitrogen analyses of 17 lakes in parts per million, based on one sample except as otherwise noted.

Lake	Depth	Organic N.	Free NH_3	NO_2	NO_3	References
Flathead........ average 9 samples unfiltered	100 m.	0.107	0.176	0.0	tr at mouth of Flathead River	
Erie............ average 32 samples	64	0.076	0.017	....	0.15	Fish, et al. (1929)
Mendota........	25	0.4794 average 13 samples	0.0743 average 6 samples	0.0146 average 42 samples	0.0769 average 47 samples	Domogalla, at al. (1925)
Bass............	7	....	....	0.002	0.0083	"
Devil's.......... average 3 samples	13	....	....	0.007	0.0108	"
Geneva.........	43	....	....	0.001	0.0275	"
Green........... average 2 samples	68	....	....	0.00185	0.0296	"
Kegonsa........	10	....	....	0.0	0.0211	"
Madeline........	5	....	....	0.0025	0.0154	"
Michigan........	265	....	....	0.0096	0.1041	"
Monona.........	22	....	....	0.0036	0.0509	"
Rock...........	20	....	....	0.0018	0.0313	"
Turtle..........	14	....	....	0.0042	0.0278	"
Waubesa........	11	....	....	0.0	0.0227	"
Wingra.........	4	....	....	0.0	0.040	"
Zurich..........	50	0.085	0.02	....	....	Guyer (1911)
Zurich (upper)...	......	....	....	....	0.8 ([16])	Minder (1926)
Zurich (lower)...	......	....	0.02	....	0.26 ([17])	Minder (1926)
Greifen.........	32	0.15	0.05	....	....	Guyer (1911)
Greifen.........	......	....	0.039 ([18])	....	0.08 ([18])	Minder (1926)

In comparison with the other lakes in this table it is evident that free ammonia runs considerably higher in Flathead Lake, while the nitrites and nitrates are absent, with the exception of a trace of the latter in one sample.

Two analyses of dissolved phosphate were made in March 1934 on samples of water taken near shore at widely separated points, both of which showed very slight traces of this material.

Hydrogen ion concentrations were determined by the electrometric method. The pH value of the lake water ranges from 8.21 to 8.63. This alkalinity is doubtless due to the limestone in the adjoining mountains, the source of the tributaries of the lake, coupled with the relatively small amount of decomposing material in the lake itself. Our results being limited to the summer of 1928, I can say nothing about seasonal changes in pH. There is no apparent difference in the values for surface and bottom water as is so evi-

[16] 1 sample.
[17] Average of 147 samples.
[18] Average of 8 samples.

dent in Lake Mendota (Juday et al. 1924), which is to be expected from the slight effect of the bottom ooze.

Oxygen and carbon dioxide content were determined in connection with each of the quantitative plancton determinations and are shown in Figures 4 and 6-9. These determinations were made from June 6, 1928 to February 3, 1930, with a break in winter, when very few collections were made, and in July 1929, when one water bottle was lost and consequently one series of readings omitted.

Oxygen distribution in Flathead Lake is similar to that in other oligotrophic lakes—Geneva, Switzerland; Tahoe, California; Seneca, New York; which have an abundance of the gas at all levels in all seasons; and differs distinctly from that in eutrophic lakes, such as the majority of plains lakes both here and abroad, in which oxygen in summer decreases markedly in the hypolimnion and may be entirely absent at the bottom.

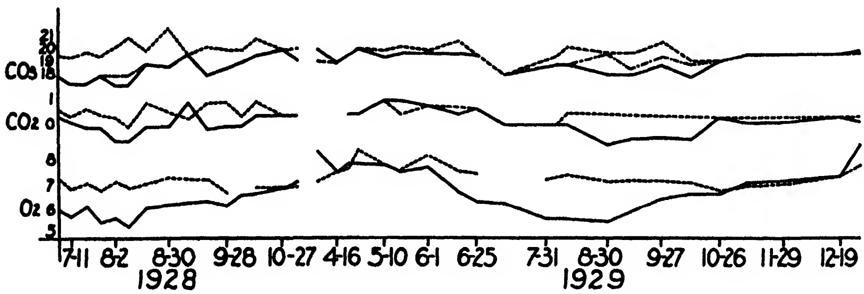

FIG. 4. Seasonal distribution of oxygen and carbon dioxide, in cc. p. l. plotted as ordinates. Dates are plotted as abscissae. The full lines indicate surface, and the dashes, bottom collections. Where the CO_3 and HCO_3 readings differ, the former is indicated by dots and dashes.

The dependence of the amount of oxygen upon temperature is clearly shown in a comparison of the curves for these two factors, for when the temperature decreases the amount of oxygen increases, and the bottom water contains a larger amount than the surface in summer, corresponding to the lower temperature there. Near the bottom, however, there is frequently a small decrease in oxygen due, undoubtedly, to decomposition (oxidation) of bottom ooze. This slight decrease, however, does not materially affect the total amount of oxygen, or its distribution in the lake, which is here determined primarily by temperature. In the Lake of Zurich, Minder's (*l.c.*) curves show a marked decrease of oxygen in summer from the surface to about 30 m., with some increase from there to the bottom. This is not explained by him, but is probably due, in part, to accumulation of zoöplancton in the thermocline and its decrease toward the bottom.

In the Attersee (Haempel, 1926) the bottom conditions apparently vary from time to time, as some of Haempel's curves show an increase, and others a decrease at this level. In winter, with the cooling of the surface as com-

pared with the bottom, the oxygen becomes higher in the former, than in the latter layer.

Organic activities (respiration, photosynthesis and decomposition) appear to play a relatively minor role in determining the oxygen content of Flathead Lake. However, a conspicuous instance of an increase in oxygen, due evidently to photosynthesis, is afforded by the data for August 9, 1928, when there was 0.2 cc. more at the 9 and 13 m. levels than at 16 m., because of a large development of Fragilaria at the former depths. This condition is similar to that recorded by Birge and Juday (1911) in Lake Mendota on September 20 and 21, 1908, and in Beasley, Long and Rainbow lakes in the summer of 1909 (l.c., Table 7, p. 43, and pls. 4, 5 and 6). It has also been described by Haempel (1926) and is evidently a rather common occurrence. We have, however, observed it only once.

During the vernal and autumnal periods of circulation, with equality in temperature between top and bottom, the oxygen is equal at the two levels for a short time at least. In Lake Mendota (*fide* Birge and Juday, *l.c.*) the surface oxygen undergoes a marked decrease in autumn due to (1) decrease in amount of phytoplancton, (2) active decay and (3) mixing of the oxygen-poor water below the thermocline with the water above, as the latter sinks, due to lowering temperature. This condition is not realized in Flathead Lake, which is further evidence of the relatively small part played by the organisms of the lake in determining its oxygen content.

Distribution of carbon dioxide (free, bound and half-bound) is shown in Figures 4 and 6-9. During spring and fall overturns there is uniformity from surface to bottom, with alkalinity developing at the surface in summer and fall, while the bottom is generally acid. The difference between these two layers in Flathead Lake, however, is rarely more than 1cc. per 1., while in eutrophic lakes it may amount to as much as 50 cc.[19]

An unusual condition developed on September 9, 1928 when the surface showed 1 cc. of free CO_2 and the bottom only 0.5 cc. At intermediate depths (3-30 m.) the water was alkaline (Fig. 4). The explanation of this condition is not clear. At first I thought my results in error, but four readings all gave distinct, though small amounts of free CO_2 at the surface. On May 18, 1929, also, a single test showed more free CO_2 at the surface than at 85m. Similar conditions are shown by Birge and Juday (l.c., Figs. 10, 29 and 31) in Lake Mendota occasionally in winter and early spring and by Minder (l.c.) in Lake Zurich (June, 1921).

The alkalinity of the surface layer in summer is more marked in areas where vegetation is more abundant than elsewhere, as pointed out by Birge and Juday (*l.c.* p. 71). We have made no tests directly in these vegetation areas, but in Hell-Roaring Bay, at Station 2, near which is an extensive plant-grown area, in August 1928 alkalinity ran from 1 to 2 cc. of CO_2 pr. 1.,

[19] Garvin Lake, Wis., 10/14/06, *fide*, Birge and Juday (*l.c.*)

while at Station 1 in the main lake it ran between 0 and 0.5 cc. at this time. Conversely, near the Somers's log boom, where thousands of logs are stored, free CO_2 runs considerably higher than elsewhere in the lake.

But little need be said regarding the distribution of the bound and half-bound CO_2. These are always equal in the lower strata of the lake and only rarely differ at the surface. They are equally distributed from top to bottom during the spring and fall overturn. During summer the amounts are usually a little lower (between 2 and 4 cc. pr. 1.) at the surface than at the bottom, while in winter there is a very slight difference (not more than 1 cc.) in favor of the surface water.

BIOLOGY—METHODS

Plancton samples were taken with the plancton trap described by Juday (1916). Thus far no one method has been devised which is wholly satisfactory for the collection and enumeration of plancton. The various methods employed have been discussed in detail elsewhere[20] and a summary of the objections to each has been given in a previous paper (Young, 1924). The trap was selected for the present investigation as most satisfactory; it is difficult, however, to compare the plancton productivity of Flathead Lake with that of other waters because other workers have usually employed the plancton net in their investigations. A comparison of the results obtained with trap and net indicates in general a considerably greater efficiency for the former.

In computing the amount of plancton various methods have been employed by previous investigators, which increases the difficulty of comparison between different waters. For a given investigation, however, where the same methods have been employed throughout, the results of the various collections are fairly comparative. Thus, while it is difficult to compare the amount of plancton in Flathead Lake with that in other lakes, the results for the former at different locations and levels of the lake, and at different seasons are fairly comparable with each other.

Our results are recorded in number of cells which, in the case of the colonial forms, makes them appear very high in comparison with those of other investigators.

Bottom samples for qualitative study were taken with a rake dredge, while for quantitative work a Birge-Eckman dredge covering an area of 1/16 m. was employed.

FLORA AND FAUNA

The flora of the lake includes several species of spermatophytes, the horsetail "fern" (Equisetum), the stonewort (Chara), one or more species of mosses and a large variety of diatoms, green and blue-green algae.

Omitting the very specialized parasitic fauna of the lake, its animal organ-

[20] Juday (1916), Reighard, in Ward and Whipple (1918), Steuer (1910) and Whipple (1927).

isms include representatives of every phylum, excepting a few, which are mainly, or exclusively marine.

The fauna is represented chiefly by protozoans, rotifers, nematodes, annelids, crustaceans, insects, molluscs and fishes; sponges hydroids, flatworms, bryozoans and mites being present in minor numbers, which, with an occasional tardigrade and gastrotrich and a few frogs, toads, turtles and muskrats, comprise the animal population of the lake.

I shall not attempt to give a detailed annotated list of species (amounting to some 700 in number), partly because of limitation of space, and partly because of incomplete identification of our collections, which comprise a number of uncertain and probably undescribed species. I shall attempt rather to indicate the salient features in the life of the lake as presented by the abundance and distribution of its characteristic forms.

BIOLOGICAL REGIONS

Without attempting to differentiate too finely between the various communities of the lake we may distinguish two main biological regions—the shallow bays and the open lake, which may, in turn, be subdivided into the littoral, pelagic and benthic areas.

A distinction between the various regions in a lake (littoral, sub-littoral pelagic, benthic and profundal) is difficult, not only because of the intergrading of the regions themselves, but also because of confusion in terminology of various authors.

The littoral as understood herein, is the region extending from the water's edge to a depth of approximately 10 m., i.e. to the limit of the larger vegetation (Potamogeton, Sagittaria, Chara etc.); the pelagic includes the remainder of the lake, while the benthic is the entire bottom, regardless of depth.

THE PELAGIC AREA

In this region may be included the major area of the deep bays with rocky shores, such as Woods and Yellow Bays in which the depth increases rapidly and conditions become very similar to those of the open lake a short distance from shore. The average depth of the open lake is about 50 m. It is a region frequently disturbed by wind in the upper layers. The exact depth to which this disturbance extends is not known, but from rather sudden changes in the level of the thermocline in summer, and from the depth at which currents may be detected, it appears to reach about 16 m.*

THE PLANCTON

The plants of the pelagic zone are almost entirely diatoms of the genera Asterionella, Fragilaria, Meloseira, Rhizosolenia, Synedra and Tabellaria

* See page 107.

with an occasional admixture of Cyclotella, Navicula, Cymbella, Campylodiscus, Surirella, Gyrosigma, Sphinctocystis, and Eunotia. Occasionally other algae occur, but these are mostly too rare to have any material influence on the ecology of this region and hence have been omitted in the charts. Of the blue-green algae Aphanizomenon, Chroöcoccus, Gomphosphaeria, Gleotrichia, Anabena, Aphanocapsa, Microcystis, Merismopedia and Spirulina are occasionally taken in open water, while the green algae are even less frequent in this region, being represented by a few specimens of Oöcystis, Sphaerocystis, Pediastrum, Cosmarium and Staurastrum. Of those forms which occur only occasionally in the plancton Chroöcoccus and Aphanocapsa are most important but even these, especially the latter, are too infrequent to play an important part.

The animals of the open lake include a limited number of common species with an admixture of several infrequent types. These are mainly flagellates, rotifers, copepods and cladocerans, with a few rhizopods and ciliates,[21] and rarely a dipterous larva, the latter probably a wanderer from the benthos. At least 90% of the animals of this region are the flagellates Ceratium and Dinobryon; the rotifers, Asplanchna, Gastropus, Notholca, Anuraea and Polyarthra; the copepods, Cyclops and Diaptomus; and the cladocerans Daphnia and Bosmina; with a few Epischura, Sida, Leptodora and very rarely Canthocamptus.

The presence of shell-bearing forms like Difflugia and Centropyxis in the plancton is interesting, since such organisms are not active swimmers and possess no obvious means of flotation. It is probable, as suggested by Steuer (*l.c.,* p. 103), that they form vacuoles of gas which decrease their specific gravity. Cyphoderia has been found in several collections from points of intermediate depth (15-21 m.) at Stations 5, 6 and 9, but always near the bottom; so that it is almost certain that this is a bottom form, which has been accidentally brought into the plancton by currents created in raising or lowering the plancton trap.

It is difficult if not impossible to arrange this assemblage in the order of dominance. The importance of any organism in the household of nature is primarily a matter of food; on the one hand, the amount which the organism consumes, and on the other, the amount which it supplies for other species. This, in turn, depends both on the abundance of the species and on its size and rate of metabolism. Regarding this last factor we know very little, though it is obvious that the more active the organism the higher will be its metabolic rate.

The lack of any quantitative collections from the areas where plants are most abundant renders it difficult or impossible to determine the relative abundance of the great majority of species in Flathead Lake. Moreover, many of them are attached or crawling forms, and there is no known method of com-

[21] Commensals on Crustacea.

paring their abundance with that of pelagic types. The best we can do, therefore, is to compare the relative frequency of various organisms in collections made in different localities at many times. By this means, and by size comparisons it is possible to draw some very general conclusions regarding the relative importance of different species in the economy of the lake.

In such a comparison perhaps *Cyclops bicuspidatus* should be given first place, although during summer and fall *Daphnia hyalina* may outrank it, because of its greater size. While the rotifers outrank the Crustacea by nearly 2:1 and the Protozoa outrank them by 500:1 in number of individuals, their greatly inferior size probably makes them of less importance in the life of the lake.

The seasonal distribution of the plancton has been studied mainly at Station 1, located at a point about 2 km. from the mouth of Yellow Bay in a depth of over 90 m. at high water. A number of collections to determine differences in regional distribution have been made at the nine other stations, but extensive seasonal studies have been made only at Station 1. The composition of the plancton and the depth distribution of its constituent forms is similar at all points studied, with the exception of Station 4 in the mouth of the Flathead River, which has a very different environment from the others.

It should be said at the outset of any discussion of seasonal distribution of the plancton that our results cover only nineteen months, from July 1928 to February 1930, while from November 3, 1928 to April 16, 1929 but one series of collections was made on February 23. A comparison of the abundance of plancton in different years must necessarily, therefore, be very incomplete. However, our 1928 collections show somewhat smaller results than do those of 1929 for the same seasons. Such a result is entirely in accord with the results of other workers. Thus Birge (1897), p. 317 says, "The feature of the annual distribution of the Crustacea which surprised me most in the progress of my work is the great difference between the numbers of the same species of Crustacea present in successive years. I do not refer so much to the larger or smaller numbers of forms like Cyclops for whose variations causes can be assigned at least in part, but rather to such facts as those shown by *Daphnia retrocurva* and by Diaphanosoma, which are either absent or present in very small numbers in one season and appear in great numbers in another year. For such variations it is very difficult to assign even conjectural causes.

"A similar fact has appeared in the succession of the algae. It is not true for Lake Mendota that the forms of algae succeed one another in a definite order in successive seasons so that one can be sure of finding certain forms at certain times of year, as would be the case with plants of woodland or prairie."

In comparing the amount of plancton at different seasons, moreover, it must be borne in mind that in computing most of our averages we have used

12 samples taken at the surface, at 1.5, 3, and at each succeeding 3 m. interval down to 31 m., and two samples at 61 and 85. m. respectively.[22] The upper 30 m. of the lake contains most of the plancton during most of the year and is the region of the greatest changes in temperature and light. But this method does not give results which are strictly comparable to each other unless the depth distribution is uniform, which it is, approximately, only in winter and spring. During the remainder of the year, when there is a higher concentration of plancton in the upper 30 m., this method raises the average as compared with that during the former season. To this discrepancy Kühl (*l.c.*, p. 143) has already called attention.

As already noted* diatoms are of chief importance in the study of the phytoplancton. The chart (Fig. 5) shows two well-marked maxima in 1929, one in May-June and the other in November-December. In 1928 the numbers were much lower on the average than in 1929, and the peaks in the curve less well defined. In this year diatoms were more numerous in August than at other seasons, with a minor rise indicated in October-November.

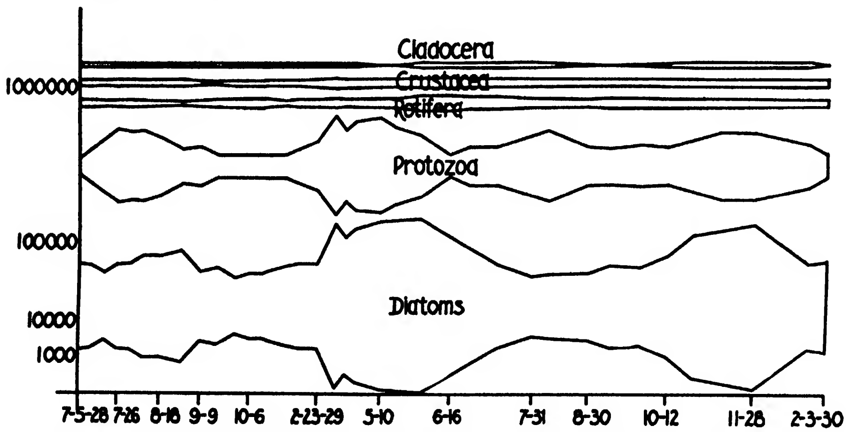

FIG. 5. Seasonal distribution of plancton. The dates are given on the horizontal, the number of organisms pr. l. on the vertical scale, which is plotted as the cube root of the latter.

Most of the diatoms are perennial, with a period of maximum development in April-June, while some (*Melosira crenulatum,* Tabellaria and Synedra) have a secondary maximum in summer or early autumn. *Fragilaria crotonesis*, however, has its major maximum in summer or autumn, with a minor maximum in spring. In 1928 it reached its peak at 12 m. on August 18, with 110,000 cells pr. l. In November of this year it had a second, smaller development, with a peak of 54,000 cells pr. l. at 6 m. at Station 6 on November 18. In 1929 it reached a peak of 30,000 cells pr. l. at 61 m. May 18, and one of 310,000 pr. l., also at 61 m., on November 28.

[22] Depths were originally measured in feet. In changing to metres, I have given the nearest integer.

* See page 117.

The autumn rise in the diatom curve for this year, and the mid-summer maximum in 1928 are due to the abundance of Fragilaria at these seasons.

Rhizosolenia is another aberrant genus in respect to its seasonal distribution. Very common during the summer of 1928 it reached a maximum of 51,000 pr. l. at 18 m. on July 26, disappearing late in September to reappear in early November. It was fairly common during June 1929, with a maximum of 10,000 pr. l. at 27 m. on June 1. After June it was usually present in scanty numbers until the following February when the work ended.

Also unlike most of the plancton Chroöcoccus has its maximum in the autumn. There are a few scattered records prior to July 31, 1929 when it became relatively common, with two fairly well defined maxima, on August 30 (11,000 pr. l. at 18 m.) and November 28 (9,500 pr. l. at 12 and 30 m.) respectively, and an intervening low point on October 12. Whether these two maxima are significant is uncertain. Further records would be required to determine this. It is interesting to note that on August 10 Chroöcoccus was high at the surface of the Flathead River near its mouth (10,500 cells pr. l.) This occurrence preceded the first maximum at Station 1 by about three weeks and very possibly contributed to it. It occurs mainly in the upper 30 m. of the lake.

Aphanocapsa is very sporadic in its occurrence, being scarcely noted in 1928, but was somewhat more frequent in 1929. Its distribution, both seasonal and vertical, is similar to that of Chroöcoccus but less regular. It reached a maximum of 8,000 pr. l. at 1.5 m. on September 11, 1929.

Considering the zoöplancton as a whole we note that the chart (fig. 5) of the seasonal distribution shows one well marked maximum in early summer with a secondary one in late autumn. In 1929 these occurred in mid June and November respectively. In 1928 our records began on July 5 and ended on November 3, so that the June and November maxima, if present, are not shown. There is, however, an indication of the latter on November 3. Early autumnal minima are shown in both years, on September 28, 1928 and October 2, 1929, with another minimum at some time in winter. While our winter records are too few to show the exact dates of the winter minimum, it is quite clear from the chart that such occurs. Besides these major waves there are several minor plancton oscillations, secondary maxima occurring in July and early October of 1929, and in April, May, July and September of 1929, with corresponding minima at intervening periods.

The major waves of zoöplancton in Flathead Lake are thus seen to correspond fairly closely with those recorded for lakes of a similar character elsewhere.* A satisfactory explanation of these yearly changes has yet to be given, but is doubtless to be found in the interaction of the many factors which determine the physical and chemical environment of the plancton. Temperature, light and food supply are unquestionably the controlling

* See page 123.

factors in plancton development, and these factors interact one with another in very complex fashion. Thus, the food supply of the zoöplancton is composed of bacteria, algae and members of the zoöplancton itself, as well as the organic content of the water in the case of saprozoic Protozoa.* The bacteria and algae in turn depend upon this organic content for food and this is furnished in part by animal excreta and by the decaying bodies of the animals themselves. Light determines, in large measure, the growth of algae and thus contributes to the food of the zoöplancton.

The basis of the food supply is the carbon and nitrogen dissolved in the water. There appears to be an ample supply of HCO_3 present at all times for the phytoplancton, and, probably N as NH_3 is always present in small amounts; but, as already indicated, our results are too fragmentary to tell much about the latter element. Oxygen is abundant at all seasons and hence need not be considered here. Temperature and light are probably the major factors in producing the spring increase, and it is possible that they also determine the increase in the fall. In spring and fall it is not unlikely that these factors reach their optimum. With increasing clearness of the water, light penetration reaches its maximum in the fall,** while in summer the high temperature is probably unfavorable for the diatoms, which accordingly decrease in number, with resultant decrease in the animals which feed upon them. In 1929 the maximum of the diatoms and Protozoa occurred in April-May being succeeded by that of the Metazoa in June; while the Protozoa minimum in June and that of the diatoms in July-August was followed by that of the Metazoa in late August. The poorly marked maximum of the Metazoa in November of this year coincides closely with better marked maxima of the Protista at this time. In 1928 the curves of the Protozoa and the diatoms follow each other rather closely and the same is true in the spring and fall of 1929, but in August of this year there was a well marked minor maximum of the Protozoa coincident with the mid-summer minimum of the diatoms.[23]

It is generally assumed that the metazoan plancton uses the phytoplancton for food. This assumption has, however, been questioned by Naumann (1921) and others, who assume, either that the zoöplancton and even fishes (Kostomarov, 1928) absorb nutriment from the water, or that organic detritus serves as food. Kühl (*l.c.*, p. 144) has discussed this question in some detail, and I shall not consider it here further than to emphasize the fact that our knowledge of the food relations of the plancton at present is too inadequate to enable us to draw any certain conclusion regarding the dependence of one form upon another in the seasonal cycle. Furthermore, it is not unlikely that the factor or factors determining abundance at one season are different from

* See page 112.
** See page 103.
[23] This discussion is based on the distribution of Dinobryon, which, in respect to cells, far outnumbers all the rest of the Protozoa. The distribution of Ceratium and Difflugia is still different, while Peridinium and Mallomonas, the other two principal Protozoa in the plancton are present in relatively insignificant numbers.

those which determine it at another. According to Thienemann (1926), Minder (1926) etc., Liebig's "law of the least" applies here; namely, that, given a number of factors (food, temperature, light, etc.), that factor which is least in amount is critical for the abundance of any species.

The seasonal distribution of fresh water diatoms has been discussed by Whipple (1927), who has pointed out the complicated nature of the problem, and the important relation of temperature, light and solutes (oxygen, nitrogen, etc.) to their development. According to this author diatom maxima occur in spring and fall during the periods of vertical circulation of the water, at which times dissolved food materials, as well as diatoms (or their spores) which have lain dormant at the bottom during winter and summer stagnation periods, are carried to the surface, where conditions of light and temperature are encountered which are favorable to the increase of diatoms. With cessation of circulation and subsequent stratification the diatoms gradually sink into lower regions, where conditions are less favorable for their growth, and there "remain dormant through another period of stagnation" (*l.c.*, p. 232).

A similar relation between periods of circulation and stagnation and the development of phytoplancton has been described by Lozeron (1902) and Minder (1926) for the Lake of Zurich. Bachmann (1911, p. 156), on the other hand, says regarding this theory that "Im Vierwaldstattersee und in den grossen südlichen Schweizerseen müssen wir nach andern Ursachen suchen, welche den Diatomeenmaxima zu grunde liegen." And Flück (1927, p. 40) agrees that there is "keinerlei Beeinflussung der vertikalen Verteilung durch diese Strömungen."

In Flathead Lake the seasonal distribution of diatoms agrees well with this theory; but their increase in August 1928 when the lake temperature was at a maximum and the thermocline was well established can not be explained in this manner. This increase was due, in part, at least to Rhizosolenia whose peculiar behavior has been discussed above.*

A di-cyclic type of plancton development has been noted by many authors in the Swiss lakes, while, according to Robert (1919), the Baltic lakes have a mono-cyclic type. The former are deep, cold lakes, the latter comparatively warm and shallow ones. Lake Mendota, however, (Birge, *l.c.*, and Birge and Juday, 1922) has a di-cyclic type, and the same is shown in the plancton curve given by Steuer (*l.c.*, p. 553, from Fuhrmann) for the lake of Plön in Germany. Both of these are lakes of the Baltic (eutrophic) type. So it is evident that no invariable relation can be established between the type of plancton development and the physical type of lake concerned.

The depth of lakes has an important influence on the life histories of their inhabitants. According to Wesenberg-Lund[24] certain species of rotifers reach

* See page 121.
[24] Fide Steuer (*l.c.* p. 296).

their maximum several weeks earlier in smaller lakes than in neighboring larger ones, and along the shores of the latter about a week earlier than in deeper parts. In my opinion this difference is due to temperature rather than to any direct effect of depth upon development.

The table given by Bachmann (1911, p. 154) shows the marked variations which may exist, not only between different species in the same lake, but also in the same species in different lakes in respect to the times of maximum development. While it is true that lakes of similar physical type show generally similar biological conditions, nevertheless each lake has its own individual character, comparable, in a way, to the individuality of the members of any biological group or "species".

A similar opinion relative to the bottom faunas of lakes is expressed by Lundbeck (1926, p. 186) who says: "Die Mannigfaltigkeit und Veränderlichkeit der einzelnen Faktoren können sich zu so zahlreichen Kombinationen zusammenschliessen, dass fast jeder See ein anderes Bild der Verteilung der Lebewesen des Bodens bietet." And Guyer (1911, p. 378) says: "Die obigen Vergleiche ergabern, dass in bezug auf das Eintreten der Maxima der verschiedenen Planktonten in den verschiedenen Seen grosse Unterschiede bestehen, und wenn wir die jeweiligen physikalischen Verhältnisse des Mediums ins Auge fassen, so finden wir, dass gerade die Temperatur der variabelste aller Faktoren ist und ganz ähnlich auch die Intensität des Lichtes ändert. Es fragt sich nun, ob wirklich so und so viele biologisch verschiedene Rassen einer und derselben Spezies existieren, oder ob nur die jeweiligen Unterschiede in der Beschaffenheit des Mediums die Änderung der Maximazeiten bedingen."

Another factor, of which we are deeply ignorant at present and which has accordingly received but scant consideration, is the length of life of plancton animals. The life span of any organism is, in general, though with many exceptions, proportional to its size.[25] "Needham and Lloyd (1916) state that 'the rotifer, Hydatina is said to have a length of life of some thirteen days', but give no authority for their statement. Steuer (*l.c.*, p. 269) gives the ages of a few copepods the average being 13 months. This figure appears high for the average life span of fresh water copepods. Judging from the curves for Devils Lake and for Lake Mendota and Green Lake, Wis., as given by Birge (1897) and Marsh (1898) the average is very much less than this. But the facts, so far as known at present, do not warrant any final conclusion." (Young 1924, pp. 45-6).

Walter (1922) describes two varieties of Cyclops viridis, one with a life span of 7-9 months and another with a span of 4-6 months, the males in each case being shorter-lived than the females. The former variety is hatched from November to February and the latter during the rest of the year. Probably

[25] See Minot (1908, p. 227).

the smaller copepods have a life span of 4-6 months, while Diaptomus vulgaris lives for 10-13 months.

Robert (1919), after reviewing the work of several authors, together with his own, reaches the conclusion (p. 41) that "Nous ne pensons pas qu'un seul des facteurs généralement invoqués: temperature, circulation ou stratifications des eaux, puisse a lui seul expliquer la date d'apparition des maxima et minima du plancton. Ceux-ci dependent sans doute de facteurs fort complexes et difficiles a isoler, parmi lesquels ceux que nous avons étudiés jouent probablement un certain role."

The above discussion, however, while offering some possible explanations for the major cycles of plancton development, will not explain the numerous minor fluctuations which appear in any yearly curve of plancton abundance. It is possible that these fluctuations are more apparent than real, due to errors in making or in counting the collections; or, which is more probable, to irregularities in distribution of the organisms themselves.

The horizontal distribution of the plancton has been studied by many authors with divergent results; but the general conclusion is that, barring occasional swarms, which are found chiefly among the Cladocera, and given similar environmental conditions, this distribution is reasonably uniform. Indeed the whole procedure of plancton study is based on this fundamental assumption. Numerous and large variations have been found, however, in both vertical and seasonal distribution of the zoöplancton by various investigators, which are more readily explained by the assumption of an irregular horizontal distribution than in any other way. Such an assumption does not, of course, imply that the horizontal distribution is *always* irregular but only that it *may* be so at times.

Examples of irregularity of vertical distribution are shown in the curves of the Crustacea and nauplii in Lake Mendota on September 8, 1896 (Birge, *l.c.,* Pl. 42). "According to these there were more adult Crustacea by about 35% at the 6 than at the 4 m. level, and slightly more at 3 than at 2 m., in spite of the fact that they were decreasing rapidly from above downward, except in the first half metre. The nauplii vice versa, while increasing from above downward, were nearly 50% fewer at the 4 than at the 3 m. level.

"Again consider the Diaptomus charts of Marsh (1898, Pl. 7). In August 1896 there occurred, according to the chart, two well marked maxima and minima with numbers ranging from 1563 to 3803,[26] a difference of nearly 150%. Similar, though less marked irregularities are shown in the curves of Birge (*l.c.*)" (Young, *l.c.*, pp. 42-3), and in those of the Wisconsin lakes given by Birge and Juday (1911) and the Finger Lakes of New York (*ibid.,* 1914). These authors consider them evidence of stratification of the organisms concerned. They deny the likelihood of their causation through errors in collection or counting, but apparently overlook the possibility of irregu-

[26] Total catch.

larity in horizontal distribution being responsible for an *apparent* irregularity in vertical distribution, nor do these authors attempt an explanation, merely contenting themselves with the statement that "such results . . . should be expected . . ." (1911, p. 116).

Behrens (1914) has shown the marked variation which may occur in the number of crustaceans occupying a given layer of water at different times, the number at night being from 200-400% higher than during the day. He attributes these differences to a retreat of these organisms to the bottom during the day time, but Kühl (*l.c.*, p. 139) attributes them on the contrary to "einer horizontal Wanderung der aktiven Schwimmer and zu dem mit passiven Transport durch Strömungen."

Marked irregularities in vertical distribution are also shown in the charts of Kemmerer et al. (1923). In Hayden Lake, Idaho, on July 7, 1911, for example, the Protozoa decreased from the surface to the 8 m. level, then suddenly increased at 10 m., with a minor decrease at 12 m. and a great increase at 15 m., with a decrease to the 40 m. level and a slight increase at 50 m. The crustaceans and diatoms also were equally erratic in their vertical distribution in these collections. Similar examples might be cited from studies of vertical distribution in any lake.

At first sight it might appear that there is no relation between irregularity in vertical and in horizontal distribution. However, it is quite evident that if the plancton *does* have an irregular horizontal distribution in the different strata of a lake and if, in a vertical series of collections one sample was taken in an area of denser population in one stratum, and another sample in one of sparser population in another stratum, then these differences in horizontal distribution might cause similar differences in vertical distribution.

A careful study of horizontal distribution of plancton in Devils Lake, N. D. has been made by Moberg (1918) who concludes that "(1) the zoöplancton in Devils Lake shows a great irregularity in horizontal distribution and this irregularity cannot be correlated with any variations in amount of phytoplancton or in the chemical and physical environment. It is more likely due to the habit of swarming among plancton animals, due perhaps to a social instinct, similar to that found in many other groups of the animal kingdom. Plancton swarms are at times visible even at considerable distances to the naked eye. (2) With larger samples (19 litres) the variations tend to be reduced, but even here they are at times greater than in the smaller ones (½ l.). (3) These variations invalidate the usual assumption that a given sample of water is representative of a large area, at least in respect to its animal inhabitants, and necessitate the collection of large numbers of samples before definite conclusions regarding their distribution or movement can be drawn." (*l.c.*, p. 264-5).

Gardiner (1931), however, in a comparison of 80 collections of Crustacea, made from a drifting ship at sea, found that 77% of them did not vary more

than ± 33% from the average, or a total range of not more than 66%, but occasional samples departed as much as 90% from the mean. This variation is considerably less than that found by Moberg (from 121% for Cyclops tó 185% for Diaptomus in two series of samples of 19 1. each), and is more nearly in accord with the results of Apstein (1896) for the Dobersdorfer lake. Both Gardiner and Apstein, however, based their results on vertical hauls with a net, which would tend to obscure any possible variations in depth distribution. Thus Gandolfi-Hornyold and Almeroth (1915) found a range of variations of 242% in the distribution of Daphnia hyalina in Lake Geneva in vertical hauls from 10 m; but when the hauls were made from a depth of 20 to 30 m. the range of variation was reduced to less than 40%.

Recently Naber (1933), by means of mathematical analysis, has shown that the differences between the averages of two series of plancton collections, one taken at the same place, and the other at different points in the same lake, all samples of both series being taken within a period of 45 minutes, are less than 3 X the probable errors of the means. He concludes therefore that there was "keine Unregelmässigkeiten in der Horizontalverbreitung die über das bei Schwankungen an der gleichen stelle zu beachtende Mass hinausgehen" (*l.c.*, p. 128). Naber's figures however show clearly that the differences between the maxima and minima of each species studied and its mean were greater than 3 X the probable error in the series taken at different points; and the same was true in many, though not all of the collections at the same point. His results, therefore appear to support my contention that plancton distribution is not uniform under uniform conditions, as is so often assumed.

In collections of ostracods in laboratory jars I have noted a tendency of these organisms to collect in "swarms" or irregular masses on the sides of the jars, and similar cases are recorded by Allee (1931) in isopods (Asellus) and brittle stars (Ophioderma). The causes of these aggregates are manifold and obscure. "Social instinct", "prototaxis", "mass protection" and "biophysical integration" are some of the vague terms which have been used in "explanation", but it must be admitted that the whole question is very uncertain at present. Enough has, however, been done to throw much doubt on the generally accepted assumption of a uniform distribution of the plancton.

Irregularities of distribution are hardly adequate, however, to explain the abruptness of some of the changes in the curves. These abrupt changes are well illustrated in the diagrams of Birge and Juday (1922) (Figs. 28, 31, 34, 35) and in those of Young (1924) (Pls. 11-19, 21, 22). The fluctuations in the latter charts from counts made by the Sedgwick- Rafter method, using only 500 cc. samples, may be due in large measure to experimental error and to local variations in distribution; but those in the former, which were based on collections ranging in amount fróm 700-1500 1.+ for the centrifuged material and from 200 to 38,000 1. for the material strained by the net, are

hardly attributable to such factors. The collections being made at the same, or very closely adjacent points, variation in location will not explain the changes. Another possible explanation is the brevity of the life cycle and rapidity of growth of most plancton forms to which reference has already been made.*

Assuming a brief life cycle and rapid growth under favorable conditions, one can readily understand such large and sudden fluctuations as are shown in the figures above cited, and in our own figure 5, in which there was a sudden and large drop from the high point of April 16, 1929 to the low of April 21, with a subsequent rise from April 27 to May 10. In this case the curves represent an average of 14 samples of 25 l. each, taken at various depths from the surface to 85 m. Variations in horizontal distribution, all in the same direction, in the several groups of organisms represented are eliminated by the law of chance, and there was no constant wind during the period involved to possibly account for movement of the plancton as a whole, so that the only explanation apparent is the death of a large part of the organisms present on April 16 and the appearance of a new generation between April 21 and May 10.

As shown in Figure 5 the four major groups of zoöplancton roughly parallel each other in their annual distribution with, however, many minor variations. Each has its major maximum in April-June with a minor maximum in October-November, but the exact dates on which these occur naturally differ for each group, and, in all probability, from year to year, although our studies are not extensive enough to determine this point.

The seasonal distribution is different for different members of the plancton. Some types are perennial and others strictly seasonal in occurrence. The former include Dinobryon, Diaptomus,[27] Cyclops, Anuraea and Notholca. Nauplii, as would be expected from the occurrence of the parent forms, are perennial, while Ceratium, Difflugia, Asplanchna, Gastropus, Polyarthra, Daphnia, Bosmina and several others are seasonal.

Most zoöplanctonts have their maximum in June. Ceratium, Difflugia and Gastropus are, however, exceptions, their maximum occurring in September-October. Daphnia and Bosmina are so uncommon at all seasons that it is difficult to assign them any definite maximum. They have two seasons, however, June-July and October and are very rare or absent in winter and spring. Polyarthra also is a warm weather form, being very rare when the temperature of the water is near 4.°

The maximum of Ceratium in Flathead Lake occurs considerably later than is usual, it being ordinarily a typical summer form, although it is not limited to this season. Thus in the Greifensee (Guyer, 1911) it has two maxima, a major one in July and another minor one in December, while a

* See page 124.
[27] Very rare during the autumn.

similar seasonal distribution is found in many Swiss lakes, according to this author.

Peridinium is rare, being seldom found in the plancton in 1928. In 1929 it had a maximum between April 16 and June 16, reaching a peak of 600 pr. l. at 18 m. depth on June 1. From June 27 to February 3, 1930 it was very rare, though usually present in a few collections of each series.

Mallomonas is still more rare than Peridinium. Curiously enough its maximum period was in August 1928 with a peak of 500 pr. l. at 12 m. on August 9. It occurred in a few collections of each series from April 16 to June 1, 1929 and thereafter was rarely seen. This seasonal distribution is very different from that in the Lake of the Four Cantons where, according to Bachmann (1911) Mallomonas has its maximum in winter. In the latter lake, however, the species (*producta* and *acaroides*) are different from that (*caudata*) in Flathead Lake, which may, possibly, explain the difference in seasonal maxima.

Actinophrys sol occurred sparingly in the plancton from August to December with a maximum of 300 pr. l. at 12 m. on August 30, 1929.

Other protozoans occasionally encountered in the plancton are *Arcella vulgaris, Centropyxis aculeata, Cyphoderia ampulla, Euglypha alveolata, Vampyrella lateritia* and Anisonema.

The succession of some forms is very striking. It is as if one organism held sway for a brief period and then stepped aside to make way for another. This is particularly noticeable in the distribution of Ceratium and Difflugia, and Asplanchna and Gastropus. From June 1 to November 28, 1929 Ceratium was present in scattering numbers during June and July, increasing in abundance in August, and in large numbers in September-October. In November it fell off rapidly in numbers and was very rare in winter. Difflugia, on the other hand, was present in small numbers from February to May, reappearing in September and continuing till February 1930, with a rather well marked maximum in December. Asplanchna was present from February to July 1929, while Gastropus appeared in very small numbers in the July 12 collection and continued until February 1930, with a rather poorly marked maximum in early September. The reasons for these successions is undoubtedly to be sought in the general environment rather than in any close interrelation between the forms concerned.

The seasonal distribution of the nauplii closely parallels that of the parent forms, Cyclops and Diaptomus; their number, however, averages somewhat greater than that of the parents, indicating a high immature death rate.

The sex ratio of certain forms shows marked seasonal variations. On April 16, 1929 the ratio for Cyclops was 67♀s to 7♂s. This proportion of approximately 10:1 gradually increased, with an exceptional drop of 10:6 on August 9, until September when the ♂s had nearly disappeared. On October

26, however, the ratio was 76:5 and continued at approximately 80:3 until the completion of the plancton work on February 3, 1930.

In Diaptomus the number of ♀s far outranks that of the ♂s during most of the year, but in late autumn and early winter the proportion of the sexes is more nearly equal. In mid-July 1928 the ratio of the sexes was 159♀s to 7♂s on the 11th and 30♀s to 5♂s on the 19th. On the 26th ♂s were not noted and were absent in the counts from then on to September 28 when one was noted. Meantime the number of ♀s had also diminished very greatly, ranging from 3 to 0 pr. l. from August 30 to November 3. On the latter date the ratio of ♀s to ♂s was 2:1. By February 23, 1929 the ratio had risen to 7:1. During June and July there was a slow and irregular increase in the ratio until August 30 when males were absent in the counts, and remained so until late November with the exception of a single individual on October 26. On November 28, however, ♂s were present in considerable numbers, the ratio of ♀s to ♂s falling to 13:9½ on the latter date, but rising again to 12:2½ on February 3, 1930 when the collections ceased.

These ratios indicate that during most of the year reproduction in the copepods is preponderantly parthenogenetic and about exclusively so in late summer and early autumn. During the colder seasons of the year and extending from spring into mid-summer, bi-sexual reproduction occurs to some extent, but even then parthenogenesis is probably the chief method. Birge (*l.c.*, p. 340) has observed that in Lake Mendota Daphnia hyalina has almost completely lost the capacity for sexual reproduction, "males never exceeding 4% of the number of females and rarely being as numerous as this." In our collections this species, which forms the major part of the Cladocera, has a distinct period of sexual reproduction in the autumn, the males averaging about 20% to 80% of females at this season.

Our results for both Copepods and Cladocera in respect to the sex ratio, agree quite closely with those of Kühl (*l.c.*) for the Walchensee in Bavaria.

In respect to reproductive cycles of the Cladocera, Flathead Lake resembles those alpine lakes in which, according to Wesenberg-Lund (1908), reproduction is di-cyclic, while Lake Mendota resembles the sub-alpine and Baltic lakes in which "there is a decided tendency to a-cycly" (*l.c.*, p. 316).

The vertical distribution of the various planctonts, collectively and individually, is very irregular, all of the distribution curves having a zigzag form (Figs. 6-9.) This type of curve is conspicuous in all diagrams of vertical distribution and is probably due to inequality in horizontal distribution in spite of the generally held opinion to the contrary, as pointed out elsewhere in this paper.*

Naturally no two organisms have exactly the same vertical distribution,

* See page 126.

nor is the distribution of any species necessarily the same at different seasons or even at closely approximate dates, which latter fact may also be due in part at least to variations in horizontal distribution already discussed.

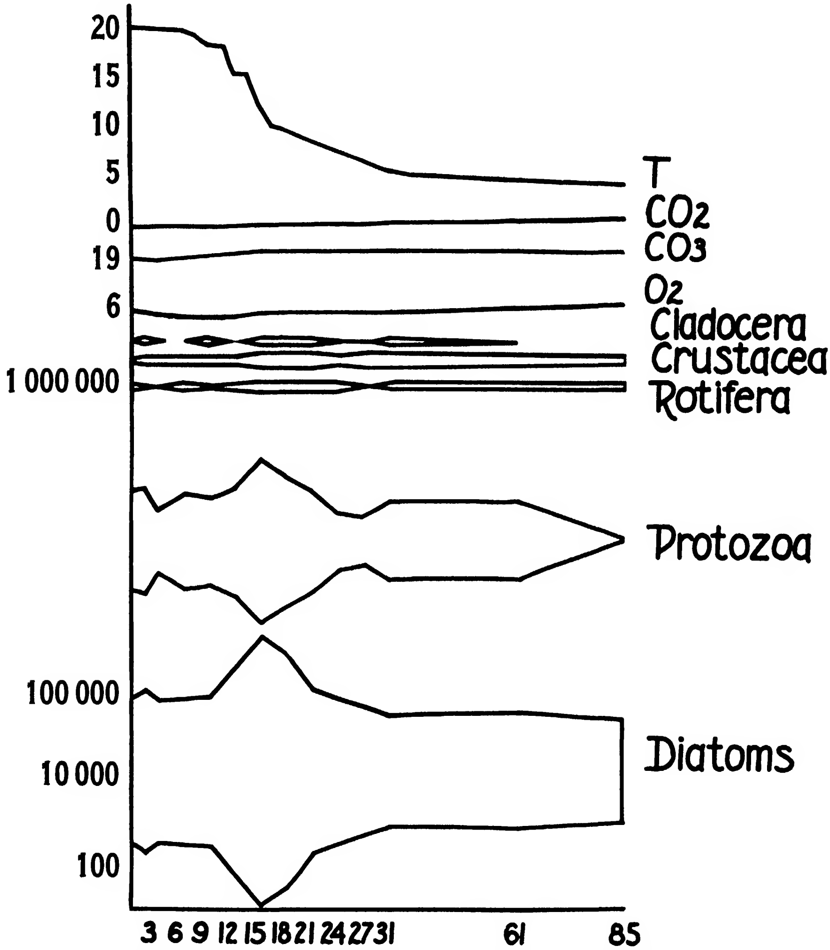

FIG. 6. Vertical distribution of plancton, temperature, and dissolved gases at Station 1, August 18, 1928. Temperatures and gases are plotted to an arithmetic, plancton to a spherical scale (i.e., as the cube root of the number of organisms). Vertical scales for all variables are shown on the chart, temperatures in degrees centigrade, gases in cc. pr. l. Depths are shown to the nearest meter, the scale below 31 m. being one half that above 31 m.

The vertical distribution of the various phytoplanctonts is, in general, similar. During winter and spring the distribution from top to bottom is approximately equal, but, with rising temperature and increasing light in June, they recede from the surface and present a maximum somewhere between 15 and 30 m. Most of the zoöplanctonts have a more or less similar type of distribution, with a low point near the surface, a maximum some-

where above the 30 m. mark and a rather sharp decrease in this region with small numbers from there to the bottom. The absence of samples between 31 and 61 m. in most of our collections probably does not invalidate this general conclusion, since in those collections which do have samples from intermediate depths, the same general results are found. A secondary maximum may, however, occur below 31 m. and in one case (nauplii—8/9/28) the maximum occurred at 49 m.

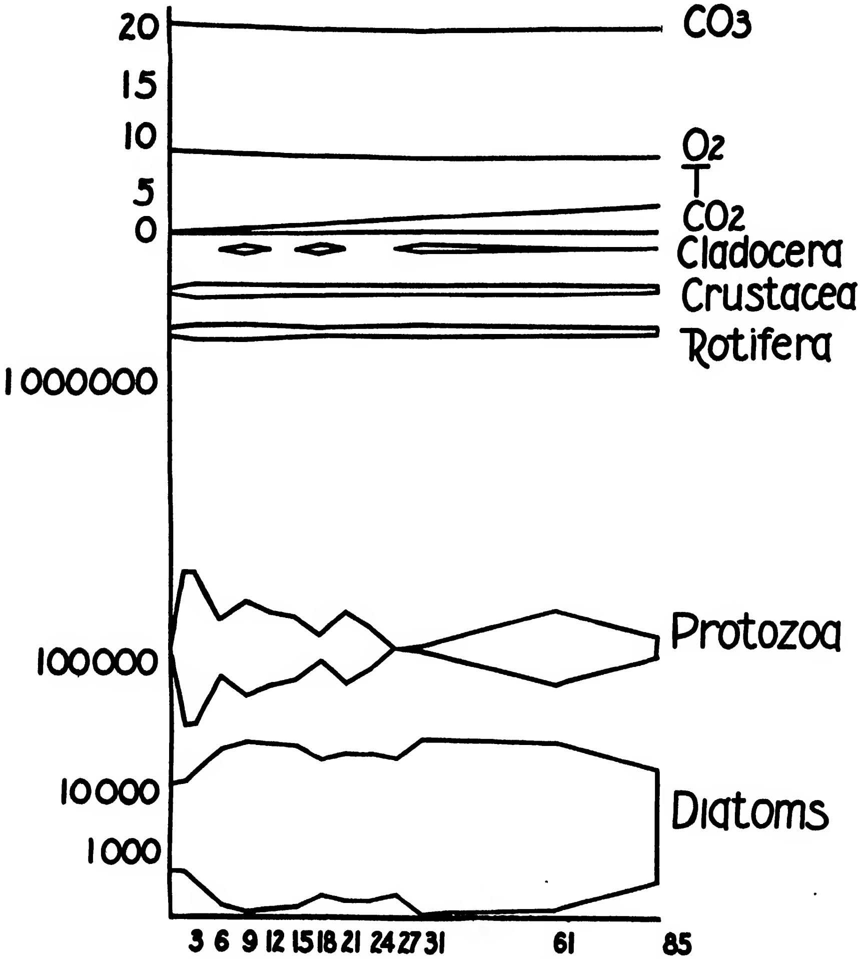

FIG. 7. Vertical distribution of plancton, temperature and gases at Station 1, February 23, 1929. For description see Fig. 6.

While most zoöplanctonts have their maximum between 10 and 30 m. and thus within the limits of the thermocline, with relatively small numbers in the upper levels, Ceratium has its maximum always in the upper 20 and usually in the upper 15 m., and is frequently present in large numbers near

the surface. Dinobyon also is occasionally abundant at the surface. Difflugia, on the contrary, while scarce at all levels, is usually more numerous below 15 m.

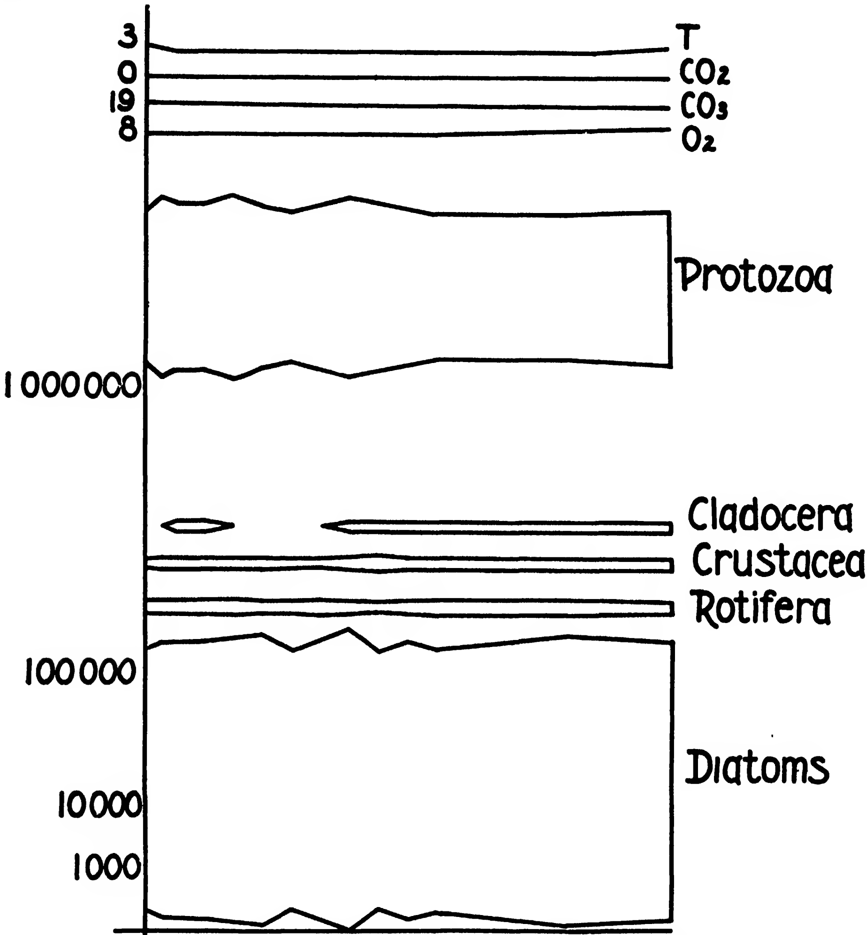

FIG. 8. Vertical distribution of plancton, temperature and gases at Station 1, April 27, 1929. For description see Fig. 6.

When the temperature of the lake approximates 4°, however, the distribution curve of most species straightens out, that is, the species becomes more uniform in distribution from top to bottom, or may even increase conspicuously in the lower levels, as was the case on April 16, 1929 where each species charted had its maximum at some point below 30 m. Anuraea, however, presents a rather marked exception to the rule of more uniform distribution in the colder water, for in February of both years (1929-30) it had a distinct maximum at 6 m. By April, 1929, however, it had moved down-

ward, at which time its distribution conformed more nearly to that of the other zoöplanctonts.

While all of the distribution curves show marked irregularity, there is generally more or less of a gradual approach to, and recession from the maxima and minima. The numbers do not ordinarily jump from zero to

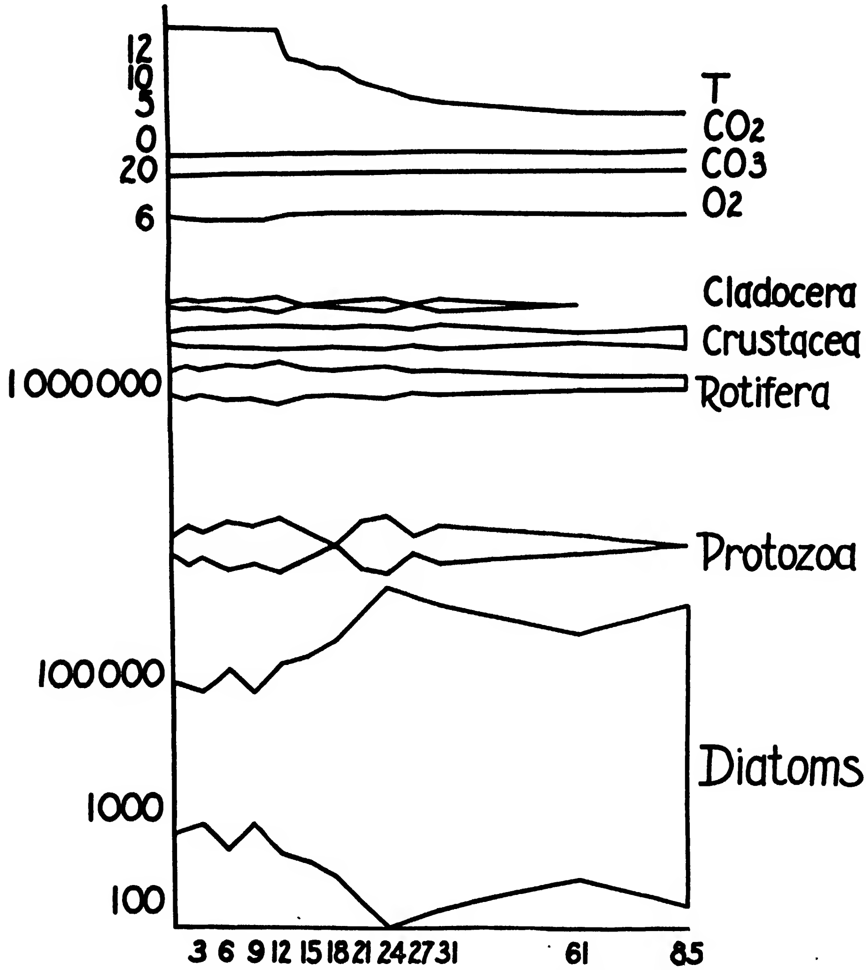

FIG. 9. Vertical distribution of plancton, temperature and gases at Station 1, June 16, 1929. For description see Fig. 6.

the maximum or vice versa in a 3 m. interval. But this happened in the case of Gastropus on August 9, 1928 when this species, which was absent in the upper 10 m., suddenly appeared in the amount of 51 pr. l. at 12 m., decreasing rapidly from here to 21 m. and disappearing about the 24 m. level.

Birge (1897) and Birge and Juday (1914) have called attention to two types of vertical distribution with respect to the thermocline. In one type

the zoöplancton is scarce in the hypolimnion and in the other is present there in considerable quantities. The former type of distribution may be due either to scarcity of oxygen or of food in the hypolimnion, while the latter type is due to an ample supply of both in this layer. According to Birge and Juday (*l.c.*, p. 588) the "chlorophyl-bearing portion of the plancton" is "confined chiefly to the epilimnion, where light conditions are most favorable", but in cold, clear, deep mountain lakes (*i.e.* Crater Lake, Oregon, and Lake Tahoe, California, Kemmerer et al., 1923) the maximum amount of phytoplancton may occur well below the thermocline. Apparently light rather than temperature is the controlling factor here.

A similar conclusion is drawn for the Walchen and Kochel lakes by Kühl (*l.c.*), who ascribes the vertical distribution of the plancton in these lakes primarily to the influence of light, while "Ein Einfluss der Sp-Sch. auf Verteilung besteht nicht" (p. 155).

Our own observations support this view, for in Flathead Lake the zone of maximum plancton development is at the lower limit of, or well below the thermocline.

According to Birge and Juday (*l.c.*) the food supply of the zoöplancton (*i.e.* the amount of chlorophyllaceous organisms) present in the hypolimnion depends directly on the amount produced in the epilimnion and inversely on the amount consumed by the zoöplancton there present.

In Flathead Lake the vertical distribution of the zoöplancton is intermediate between these two types. While the population of the hypolimnion is in general much less numerous than that of the epilimnion and the thermocline, it always contains a considerable number of planctonts. The vertical distribution of the plancton is clearly a resultant of three factors, food, light and temperature.

Hofer (1899) in a study of several mountain lakes of Austria and Germany maintains the existence of an abyssal lifeless region in all deep lakes. But this is denied by Kühl (*l.c.*), who has shown an increase in the number of copepods at certain times in the 175-190 m. level in the Walchen Lake, which has a maximum depth of 192 m. It is refuted also by the distribution of life in Lakes Baikal and Tanganyika (Thienemann 1925).

Birge (*l.c.*) finds the young Crustacea nearer the surface than the older ones. While we have not made a careful study of this question, our observations differ from those of Birge. In general the larval copepods (both nauplii and later stages) average deeper in their distribution than do the older stages, while there is no evident difference in the distribution of the young and adult Cladocera. As Naber (1933, p. 96) points out there is no constant relationship in this regard.

Our collections at stations other than No. 1 are too few to enable me to draw any very definite conclusions regarding the horizontal distribution

of the plancton in Flathead Lake. A priori it was expected that the shallow bays (Stations 2, 3, 8, 9, 10) would show much higher results than the open lake, because shallow waters are, in general, more productive of plancton than are deeper ones, and because of the higher aquatic vegetation which is more or less abundant in the bays. It should be borne in mind, however, that the quantitative collections were necessarily made outside, though in rather close proximity to the areas of dense vegetation; and, consequently, the amount of life within the latter is not shown. In general, however, our expectation has not been realized. In some cases the shallow water collections show much higher results than do those from deeper water, especially among the rotifers and diatoms, but the results are by no means consistent. Station 8, for example, at the mouth of the Swan River, gives results which are generally low as compared with those at Station 1 in the open lake, with the exception of Dinobryon, which in three of the five collections was higher, and in two lower in number than at Station 1 on the approximate dates. Asterionella also is exceptional, for it reached a peak of 404,000 cells pr. 1. at 1.5 m. depth on July 2, 1929, while at Station 1 on June 27 its maximum was 65,000 pr. 1. at 30 m., and on July 12, 43,000 at 27 m.

The comparative results show clearly the inequalities which may exist at different stations at corresponding times. Thus, on July 4-5, 1929 there were great numbers of Anuraea and Notholca present at the southern and western ends of the lake (between Hell-Roaring Bay and Dayton), while on July 2, 1929 at the northern end of the lake (Somers) the numbers were much smaller.[28] At the mouth of a tiny creek near Dayton on July 4, 1929 the relatively enormous number of 296 Bosmina pr. 1. were present in the surface water, while this genus has never numbered more than 13 pr. 1. in any sample from any other point, with the exception of Station 10 (near Elmo); where, on this same date, it numbered 50 pr. 1. at the surface. Several other instances of the same sort could be cited, but these are, perhaps, the most striking cases, and serve to illustrate well the usual inequality in distribution at various points. Here, of course, we are dealing with distribution in somewhat different environments. Regarding inequalities of distribution in the same environment see page 125 *et seq.*

Reparding the relative abundance of plancton at the periphery and the center of a lake differences of opinion exist. Thus Linder (1904) believes that the latter is the more populous area, but this opinion has not been supported by Guyer (*l.c.*), and in my own work (Young, 1924) I was unable to find any consistent differences in amount of plancton at the shore and at some distance therefrom.

[28] At Station 2 in Hell-Roaring Bay on July 5, 1929, Notholca averaged 381 pr. 1.; at Station 3, Somers, on July 2, 1929, 18 pr. 1.; while for the same places and dates Anurea averaged 332 and 11 pr. l. respectively.

THE LITTORAL AREA

As already stated,* in the littoral area may be included all of the shore area to a depth rather arbitrarily taken at 10 m. Most of this region consists of rocky, wave-beaten shores with a rather distinct drop-off. A little of the shore has gravel beaches, while at the northern end of the lake the Flathead River delta has formed a rather extensive sandy shore.

Submerged rocks and logs near the shore are covered with a slimy growth of stalked diatoms (Gomphonema, Cymbella) and filamentous green algae (Bulbochaetae, Oedogonium, etc.).

The principal animal inhabtants of the rocky shores are insect larvae and molluscs. The former are chiefly Ephemerida and Trichoptera with occasional Plecoptera; and the latter Lymnea, Physa, Planorbis and Valvata, of which the first is the most numerous.

Capsules of the leech (*Herpobdella punctata*) are found commonly on the rocky shores, mainly at depths less than a metre, while animals of occasional occurrence are Hydra, Fredericella, Spongilla, Gammarus, Chiromonids, annelids, planarians and a host of species including Protozoa, rotifers, copepods, cladocerans, etc., many of which are doubtless adventitious, being carried in from the open lake by currents.

The sandy beaches near the Flathead River inlet have not been very thoroughly studied. Lacking any protection from the heavy surf to which they are often exposed, they appear to have no macroscopic life whatever.

THE BAYS

I have already made some comparison between the life of the bays and that of the open lake.* The collections on which this comparison was based were necessarily, however, made in open water and revealed nothing of the life which inhabits the shore line and the plant societies (Scirpus, Potamogeton, etc.) In these habitats, especially the latter, occur all the lake inhabitants with the exception of some of the fishes, while fully 90% of them are restricted to these habitats.

The bays differ widely in character. Many, such as Woods and Yellow bays, are essentially nothing more than deeper or shallower indentations in the general shore line, and, aside from providing protection from wind and a settling place for water-logged forest debris, afford a habitat similar to that of the open lake. Others, of which Hell-Roaring Bay is the most striking example, are shallow, with gently sloping muddy bottoms, which support a luxuriant growth of various aquatic plants. The former differ but little in their biotas from the open lake, but the latter support a large assemblage of forms, most of which seldom occur in deep water, while many are never found there. The bottom of the shallow bays is submerged at high water in

* See page 117.
* See page 136.

early summer, but with the recession of the lake in late summer and fall, extensive areas are exposed. These bays offer a suitable habitat for the various species of aquatic seed plants which occur in the lake, most common of which are the following: "*Scripus validus, Batrachium trichophyllum, Polygonum amphibium, Sagittaria cristata, Eleocharis palustris, Acorus calamus, Hippurus vulgaris, Myriophyllum verticillatum, Typha latifolia, Potamogeton natans, P. pectinatus, P. perfoliatus, P. filiformis, P. compressus,* and *P. heterophyllum.* In addition to these aquatic seed plants the scouring rush (Equisetum) is found in the same regions.

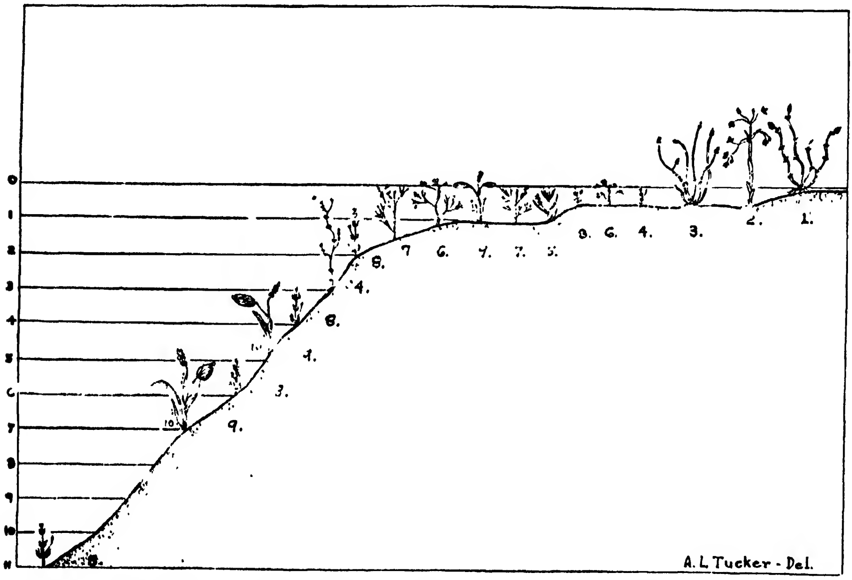

FIG. 10. Distribution of the larger aquatic vegetation on the lake shore. The steepness of slope of the lake bottom is necessarily much exaggerated.

1. Equisetum sp.
2. Scirpus validus
3. Eleocharis palustris
4. Myriophyllum verticillatum
5. Potamogeton compressus
6. Batrachium trichophyllum
7. Potamogeton pectinatus
8. Chara sp.
9. Potamogeton natans
10. Attached forms of various algae

Such plants as these crowd the shore line but rapidly diminish in numbers in deepening water. They grow more numerously at the edge of the water because of abundance of air, moisture and light, while a few can grow wholly submerged. None of them can endure the beating of the waves on exposed shores such as are so prevalent in this lake. Thus it is that the scarcity of sheltered bays acts as the limiting factor to the number of the higher aquatic plants found in Flathead Lake. As a concrete illustration of the distribution of such aquatics along the shore line, the following diagram (Fig. 10) will serve to show the association of such plants. This diagram, though illustrating the life zones of the higher plants at Big Fork, is typical of the other bays in the lake to a greater or lesser degree.

The low flats exposed at low water are covered with species of Equisetum, Scirpus, Eleocharis and Typha. These plants while able to grow in standing water are never completely submerged. Among the submerged plants are Batrachium, Myriophyllum and Potamogeton. In addition to those mentioned the Stone-Wort (*Chara sp.*) is found in large numbers in the shallow portions of the lake growing attached to the bottom. It is usually incrusted with lime and although seldom eaten by any of the aquatic animals, it forms a shelter for them as well as a means of attachment for many forms of lower plants."[29] The stems of plants and submerged sticks and logs offer convenient attachments for numbers of filamentous algae (Cladophora, Spirogyra, Ulothrix, etc.), while floating in the sheltered waters are to be found all of the pelagic forms and a host of others.

"The numbers of these minute plant forms can be better appreciated when it is stated that fifty-one species of algae were found and identified from one collection made at Big Fork on July 5, 1929. This does not include the many species of diatoms that have not yet been identified. The same could be said for Hell-Roaring Bay for it was there that probably over one-half of the algae were collected."[29]

THE BOTTOM FAUNA

As in the case of the pelagic inhabitants of the lake, so too in that of the bottom dwellers it is difficult or impossible to draw any line between littoral species and those inhabiting the deeper water. In both cases the presence or absence of vegetation is one of the factors in limiting the distribution of littoral life. With the bottom fauna the character of the bottom and the presence of suitable hold-fasts and shelters in the form of rocks or logs are important factors in determining the distribution of species in addition to those of pressure, temperature, etc.

Our study of the bottom organisms of Flathead Lake has not been complete, but a fairly careful study of the bottom fauna has been made in Yellow Bay and the adjoining lake, for comparison with the character and amount of this life with that in lakes elsewhere. Our collections include five series for quantitative study taken in September, 1930 and March, May, July, August and September, 1932, from a depth of 1.5 m. in Yellow Bay to one of 94 m. in the open lake about 2 km. from shore, together with a few qualitative collections at several widely separated points in the lake.

The results of these collections are given in Table 10 and Figures 11-12, which show the distribution of the bottom life at various depths between Yellow Bay and Station 1 in the open lake at different times.

The bottom deposits have already been discussed,* and this discussion is presupposed in what follows here.

In the case of the inhabitants of such vegetation-rich areas as a part of

[29] Ms. notes of C. W. Waters.
* See page 97.

Hell-Roaring Bay and Big Arm near Dayton, it is difficult to tell which animals live both on the bottom and on the vegetation, and which are confined to the bottom only. We have found that those samples containing plant material give consistently higher counts than do those in which this is lacking.

TABLE 10. Distribution of bottom life in Flathead Lake at different depths and seasons.

9-4—9/8/30	Turbellaria	Nematoda [30]	Mermithidae	Oligochaeta	Hirudinea	Amphipoda	Hydracarina	Ephemerida	Trichoptera	Odonata	Coleoptera	Chironomidae	Sphaeridae	Gastropoda
9 m.	....	....	....	96	....	....	64	16	....	....	....	112	80	....
15 m.	....	....	....	48	....	....	16	....	....	....	....	224	....	....
23 m.	16	....	....	80	....	....	32	....	....	....	....	96	16	....
35 m.	....	....	....	....	....	....	....	....	....	....	....	16	....	....
49 m.	....	....	....	....	....	....	....	....	....	....	....	64	....	....
89 m.	....	....	....	....	....	....	....	....	....	....	....	16	....	....
AVERAGE [31]	3	....	....	37	....	....	28	16	....	....	....	88	16	....
3/14/32														
10 m.	16	....	....	112	....	672	16	16–32 [32]	16	32	....	2736	288	48
14–17 m.	....	....	....	40	16	....	16	....	....	....	....	768	56	....
32 m.	....	16	....	....	....	....	....	....	....	....	....	224	16	....
AVERAGE [31]	4	4	....	48	10	672	12	16–32 [32]	16	32	....	1124	104	16
5/12–15/32														
Sand 3 m.	....	....	....	....	....	....	....	....	....	....	....	48	48+ [33]	48+ [33]
9 m.	....	....	....	32+32 [33]	....	48	80	16	....	....	....	1536	16	....
17 m.	....	....	....	48+16 [33]	16	....	....	....	....	....	....	304+32 [33]	16	32
35 m.	....	....	....	.... [32–33]	....	....	16	....	....	....	....	64	....	....
AVERAGE [31]	....	....	....	20+ [33]	5	24	24	8	....	....	....	488	20	27
7–8/32														
1–1.5 m.	....	....	....	....	8	....	....	....	....	....	....	40	56	....
6–9 m.	....	....	....	40	16	40	8	....	60	8	....	276	180	52
18–24.5 m.	....	40	8	40	....	....	....	....	....	....	....	112	24	....
30 m.	....	....	....	....	....	....	....	....	....	....	....	368	....	....
55 m.	16	160	32	....	....	....	....	....	....	....	....	128	....	....
83–91 m.	....	496	....	16	....	....	....	....	....	....	....	48	8	....
AVERAGE [31]	2	103	4	16	12	20	23	....	30	4	....	147	64	26
8–9/32														
1.5 m.	8	....	....	....	....	152	....	32	8	24	32	48	56	104
9.5 m.	16 [32]	....	....	....	16	32	....	....	....	....	....	112	....	....
31 m.	....	48+16 [33]	16	....	....	....	....	....	....	....	....	288	....	....
94 m.	....	1456	64	80	....	....	....	....	....	....	....	112	....	....
AVERAGE [31]	8 [32]	376	20	20	8	92	....	16	4	12	32	140	14	52

[30] The numbers of nemas recorded in Flathead Lake are probably much too low, due to the difficulty of finding the minute organisms in the very fine ooze which covers the lake bottom, and in the earlier collections (prior to July, 1932) they were probably overlooked altogether.

[31] Averages based on number of collections down to, and including only the maximum depths at which each group occurs. Of the above groups the following are apparently restricted in distribution to the depths specified: Turbellaria, 55m., Hirudinea, 17m., Amphipoda, 10m., Hydracarina, 35m., Ephemerida, Trichoptera and Odonata, 10m., Gastropoda, 17m.

[32] Record uncertain.

[33] Fragments.

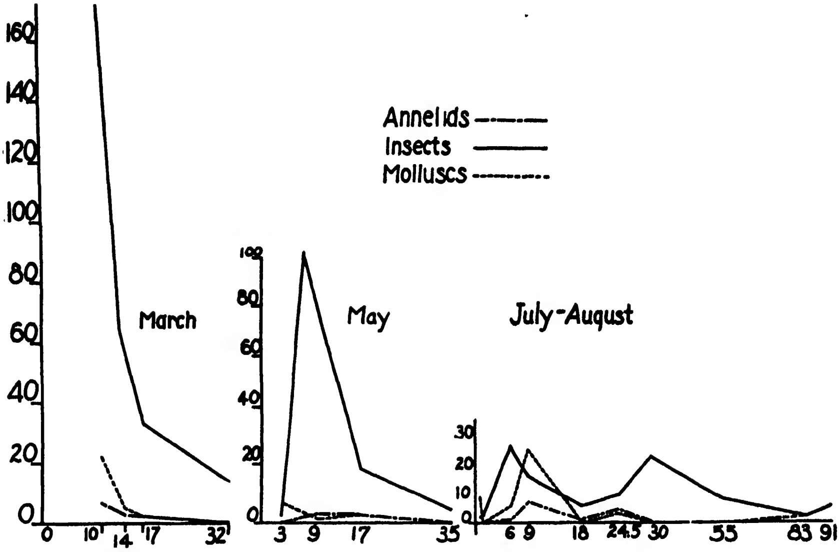

FIG. 11. Depth distribution of the bottom fauna in different months. Numbers pr. sq. m. plotted as ordinates, dates as abscissae.

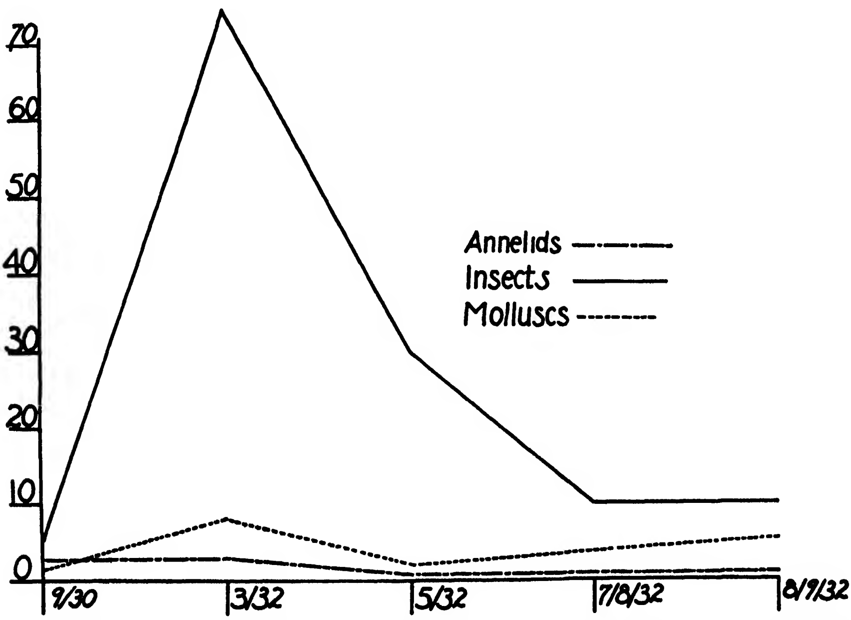

FIG. 12. Seasonal distribution of the bottom fauna. Vertical scale = number of animals pr. sq. m. The dates are given as abscissae.

In order to make a comparison between the number and kinds of animals present on the bottom, which is barren of plants, and on that which is plant covered, we have taken samples in closely adjacent areas, one covered with

Myriophyllum and the other free therefrom. Both were areas of sandy bottom at approximately equal depths (1.5 m.). The results, which are given in Table 11, show clearly the greater abundance of animals among the plants than on the comparatively plant-free areas. Dredging a mass of Chara from Yellow Bay at a depth of 8-10 m. yielded in an incomplete count 27 chironomids, 2 leeches, 1 Gammarus and 2 molluscs. From these results, incomplete though they be, it is very evident that much of the material taken in the dredge comes from the higher plants growing on the bottom, which fact must be taken into account in any study of depth distribution of animals. Even more striking is the comparison of Lundbeck (1926, p. 118) in which he gives a total of 6,622 animals pr. sq. m. at a depth of 0.5 m. on a sandy bottom covered with Chara, and 633 on a similar bottom, partly stony and without Chara.

TABLE 11. Numbers of bottom animals pr. sq. m. in two closely adjacent areas.

	In Myriophyllum	On open bottom
Hydra	64	
Hyalella	304	16
Acarina	16	
Ephemera	16	48
Trichoptera (cases)	80	16
Coleoptera	64	
Enallagma	48	
Chironomidae	32	4
Helisoma	16	
Gyraulis	112	
Valvata	64 (and one empty shell)	16
Pisidium	64 (sev. empty shells)	48 (sev. empty shells)
Total	880	192

Thienemann (1926, p. 51) says . . . "die Besiedelung des Bodens eine flachenhafte sein muss; auch der weiche Schlamm ist nur in seiner Oberfläche belebt, schon in einer Tiefe von ein paar Zentimetern hört alles Leben auf", while, according to Lundbeck (1926, p. 80) the "Bodentiere (with exception of the Tubificidae) auf die Schlamm-oberfläche beschränkt sind."

I have made a few tests to determine the accuracy of Thienemann's view by sinking a tube into the bottom and examining different depths of the core extracted by it, by collecting with a hand scoop in shallow water samples of bottom deposits from the surface and below it, and by examining samples taken with the Eckman dredge, in which the surface ooze could be readily distinguished by color from the deeper layers. These tests indicate that most of the bottom forms live in the surface layer or a very few centimetres below it. But Dorylaimus, of which vast numbers occupy the deep bottom of the lake, appears to be more abundant at a depth of 4-12 cm. in the ooze than it is above this level in the deeper parts of the lake. In such a situation their only apparent means of nutrition is by osmosis from the ooze, and of what use the spear,

which is a characteristic feature of this genus, can be, is problematical. It seems likely that they are adapting themselves to a new habitat, and that, in course of time, the spear may cease to function and degenerate, as seems to be the case with the intestine of the mermithids. Why these worms are so abundant in the deeper parts of the lake and relatively uncommon in the shallower waters is also an unsolved problem.

Omitting the sub-microscopic forms such as ostracods, cladocerans, etc., our collections show a total of at least 38 benthic animals in Flathead Lake, while a record by Forbes (1891) of Plumatella brings this number to 39. Were specific determinations possible for all of the chironomids, annelids and Trichoptera, the list would be much increased.

Of this assemblage the Chironomidae are evidently the commonest forms, with Chironomus at the head of the list. Next to the chironomids the oligochaetes and sphaerids are most numerous. The chironomids include the genera Chironomus, Tanypus, Tanytarsus, Corynoneura, Orthocladius, Bezzia and Ablabesmyia. Hyalella, which is frequently common in bottom collections, probably owes its abundance to the presence of vegetation there.

According to the classifications of Thienemann (1923) and Naumann (1927), oligotrophic lakes, to which class Flathead Lake belongs, have a Tanytarsus fauna and lack Corethra, while the eutrophic and dystrophic lakes have a Chironomus fauna and the presence of Corethra. In Flathead Lake Tanytarsus, while present in considerable numbers, is by no means the dominant midge, being outnumbered probably 2:1 by Chironomus. The absence of Corethra, however, is a striking feature of the insect fauna of the lake.

The vertical distribution shows a marked decrease in number of organisms with increase in depth. Between 25 and 35 m. bottom life mostly disappears with the exception of chironomids and nemas, an occasional annelid, planarian and, possibly, a few microscopic organisms. Thus, the bottom fauna corresponds rather closely in its depth distribution with the plancton, which, as already shown,* is generally much less abundant below than above 35 m. The factors determining the distribution of the former are probably temperature, pressure, possibly light and food and, in the case of some, shelter and hold-fasts. Lack of bottom oxygen, which undoubtedly influences the benthos in lakes of the eu- and dystrophic types, can play no part here at any season.

In Shakespeare Island Lake, Ontario, Cronk (1932) found the profundal zone (below 6 m.) "poor in species, but rich in numbers" (*l.c.*, p. 56). In Flathead Lake the same type of distribution occurs, but the "profundal" zone lies at a much greater depth, and is characterized chiefly by the nematode

* See page 132.

Dorylaimus. In Lake Nipigon on the contrary (Adamstone, 1924) the average number of bottom animals does not differ greatly at any depth.

Eggleton (1931) and Lundbeck (1926) have shown that in some lakes differences in depth distribution of benthic animals occur seasonally, the concentration zone moving deeper in winter and rising in summer. We have not observed this change in the concentration zone in Flathead Lake, but our observations are rather too limited to admit of any certain conclusions on this point.

In the Japanese lakes studied by Myadi (1931, 1932) "A comparison of the bottom fauna at different seasons of the year shows remarkable changes in the distribution of some animals and none for others. Examples of the former are larvae of some Chironomidae and of Corethra" (1931, p. 223). In the case of Corethra the young larvae settle in shallow bottoms in summer, migrating into deeper water as they become older. The reason for this is still doubtful. Myadi suggests that negative phototropism may play a part. The larvae of Endochironomus, on the contrary tend to move upward from deeper levels as the oxygen decreases therein.

Eggleton (*l.c.*) and Juday (1922) have shown a very marked seasonal periodicity of Corethra, the maximum numbers occurring in March and the minimum in August. Our observations confirm these results by showing a greater abundance of insects in the benthos in March than in May or September (Fig. 11). This difference is readily intelligible as cyclic in character, but how many broods occur every year we do not know. Muttkowski (*l.c.*, 1918) believes that there are at least three of Corethra in Lake Mendota. Lundbeck (*l.c.*, 1926), on the contrary, finds that in the lakes of northern Germany most species of bottom organisms reach their maximum in early autumn. According to this author, Chironomus bathophilus, one of the most abundant midges, has a single swarming period (May), while another common midge (C. plumosus) swarms from June to November.

Myadi (*l.c.*, p. 99) also says that "in oligotrophic lakes the population is greater in October than in July."

GENERAL DISCUSSION

An ecological study of any area, whether land or water, is of both local and general interest; of interest not only in determining the relation which exists between the members of the local community of organisms which it harbors and their environment; but also in comparing this relation with those in similar communities elsewhere, in the attempt to classify all of these communities, and to discover the general laws underlying such classification.

The ecological classification of any area must be based upon all factors—physical, chemical and biological. Thienemann (1925) has made a valuable contribution to the classification of inland waters, and I shall follow his scheme in my attempt to compare Flathead Lake with those elsewhere.

According to Thienemann, fresh water lakes may be divided into oligotrophic, eutrophic and dystrophic types. Flathead Lake clearly belongs to the first of these types which includes mountain lakes in general and is characterized by:

1. Considerable size and depth.
2. High purity.
3. Low turbidity and, vice versa, high transparency.
4. A low average temperature for the whole body of water.
5. A distinct thermocline in summer.
6. Ample oxygen at all depths.
7. A bottom temperature varying but little throughout the year.
8. A comparative poverty of plancton which is distributed mainly in the upper fourth or third of the lake.

There are many other characteristics of this type of lake but the above will amply suffice to define it.

The plancton productivity of a lake is a question of both ecological and economic interest, expressing on the one hand the ecological factors in terms of amount of life, and, on the other, determining in large degree the variety and abundance of fish, which are, after all, the final expression of the lake's fitness as a home for living things.

Table 12 shows the number of organisms pr. 1.[36] for 12 North American and one European lake compared with Flathead Lake. In compiling the table, I have selected those data which are, as nearly as possible, comparable in respect to season, although the variability in plancton abundance from season to season, and even from day to day, is so great as to render such a comparison at best only approximate. In comparing these data, furthermore, the difference in methods of collecting must be borne in mind,* as well as the small number of collections available from many lakes of similar character elsewhere.

In "Lakes of the Northwestern United States" (Kemmerer et al, *l.c.*) the authors have collected data on fifty-two lakes in Idaho, Oregon, Washington and California, showing the physical and biological conditions in these lakes with reference to fish culture therein. These lakes range from those two or three hectares in area to Lake Pend Oreille with an area of 322 sq. km.; and in depth from those of 2 m. to Crater Lake, Oregon, 610 m. deep, "the deepest known lake in the United States".

I have selected four of these (Chelan, Crater, Pend Oreille and Upper Klamath) for comparison with Flathead Lake. The three first of these are deep lakes of the oligotrophic type of Thienemann (*l.c.*) while the last is a shallow lake of the eutrophic type.

The table shows a much greater number of organisms in Flathead Lake

[36] Average for all depths.
* See page 116.

than in any of the first three lakes above mentioned, while Upper Klamath is richer in some forms, (diatoms, Protozoa, Cladocera) and poorer in others (rotifers) than Flathead Lake. The lesser number of copepods in the former is probably not significant.

In western central New York are a series of lakes occupying old river valleys which, from their elongated and roughly parallel arrangement, have been called "Finger Lakes". They have been examined rather briefly by Birge and Juday (1914, 1921) and Muenscher (1928). Several of these are large deep lakes which, in their general features, resemble Flathead Lake. From them I have selected three (Canandaigua, Cayuga and Seneca) for comparison with Flathead Lake, all of which appear to conform fairly well to the oligotrophic type of Thienemann (*l.c.*). Flathead Lake shows a somewhat larger amount of plancton than either Canandaigua or Seneca, while it has more of some organisms and less of others than Cayuga.

Recently a number of studies have been made by the University of Toronto on Lake Nipigon in Ontario, about 80 km. north of Lake Superior. This is a lake approximately 4590 sq. km. in area and about 330 m. in depth. It is clearly an oligotrophic lake, although departing therefrom in certain respects; and agrees fairly well with Flathead Lake in its general features, both chemical and physical, so far as data are available for comparison. The average summer temperature of Lake Nipigon, however, is considerably lower than that of Flathead Lake, while bicarbonate alkalinity is somewhat higher. The oxygen content is high at all depths and free Co_2 varies from 0 to 1 ppm., conditions very similar to those in Flathead Lake, as is also the pH value.

I have no data on plancton abundance in the deeper parts of Lake Nipigon, but McKay (1924) has published some on the shallow bays. These data show a somewhat larger number of rotifers but fewer diatoms and Protozoa than in Flathead Lake.

Lake Erie has at various times been the subject of much limnological work. Recently an investigation, conducted jointly by several agencies, has been undertaken "to determine the cause or causes for the decline in the fisheries", a preliminary report of which was issued in 1929 (Fish et al., 1929). Judging from the available data, Lake Erie is intermediate between lakes of the oligotrophic and those of the eutrophic type, but approaches more nearly the former. It has a distinct thermocline in summer with abundant oxygen at all depths and moderate purity, judged by the analyses of carbonate and nitrogen,[37] but depth averages and light penetration are rather low.

The data for Lake Erie are in such form that I can make no comparison of the relative number of copepods and Cladocera in it and in Flathead Lake. In respect to diatoms Flathead Lake is much higher, while the numbers of Protozoa and rotifers do not differ widely.

[37] Water from the open lake is reputed to contain only about 3 ppm. of "saline" matter. If this includes all of the inorganic salts this water must be exceptionally pure.

TABLE 12. Number of organisms pr. l. for 14 lakes.[34]

	Diatoms	Protozoa	Rotifers	Copepods	Cladocera
Flathead Lake, General average of 162 samples, plancton trap colls.	3636	58	34	16	3
Canandaigua Lake, N. Y. 8/20/10, 7/27/18. Average of 16 samples from 0 to 80 m. depth, closing net colls.	14	11	1	7	1
Seneca Lake, N. Y. 8/2/10, 8/1/18. Average of 19 samples from 0 to 170 m. depth, closing net colls.	97	17	3	14	3
Green Lake, Wis., 8/20/18. Average of 8 samples from 0 to 65 m. depth, closing net colls.	1	5	6	32	1
Lake Chelan, Wash. 8/14/11, 9/11/13. Average of 25 samples from 0 to 458 m. depth, closing net colls.	3	6	0	5	0
Crater Lake, Ore. 8/1/13, 9/5/13. Average of 24 samples from 0 to 590 m. depth, closing net colls.	7	0	1	0	0
Lake Pend Oreille, Idaho. 7/17/11, 8/28/12. Average of 16 samples from 0 to 365 m. depth, closing net colls.	0	0	0	11	3
Cayuga Lake, N. Y. 8/12/10, 7/30/18. Average of 17 samples from 0 to 120 m. depth, closing net colls.	579	264	33	5	9
Upper Klamath Lake, Ore. 7/29/13. Average of 5 samples from 0 to 10 m. depth, closing net colls.	7877	1064	1	10	7
Lake Mendota, Wis. 7/20, 8/8, 10/11/06. Average of 31 samples from 0 to 12 m. depth, pump method.	....	..	233	78	..
Lake Erie, N. Y. 8/15 - 9/14/28. Average of 144 samples, net colls.	264	113	30	..	..
Devil's Lake, N. D., 1911 - 1923. Average of approximately 300 samples ([35]), Sedgewick-Rafter Method.	....	..	350	228	..
Lake Nipigon, Ont., 6/1922-9/1923. Average of 86 samples, from 0 to 22 m. depth, closing net colls.	668	27	46	15	4
Lake Neuchatel, Switzerland. 1900 - 1920. Average of 85 samples from 0 to 80 m. depth, net colls.	....	..	56	7	0

[34] In computing the averages for diatoms and Protozoa, I have omitted the filamentous diatoms and colonial Protozoa.

[35] The data on which the averages for Devils Lake were based have been lost. Furthermore, they varied somewhat for each group. Therefore the number of samples given is only approximate.

It should also be noted that, whereas the great majority of phytoplanctonts in Flathead Lake are diatoms, in both Lakes Erie and Nipigon there is a considerable proportion of other algae.

The main limnological work in North America has been done by Birge and Juday (1911, 1922) and their co-workers on the Wisconsin Lakes, most of which are relatively shallow lakes, with a depth of less than 25 m., while only one, Green Lake, has a depth of more than 60 m. I have selected two of these for comparison—Mendota and Green Lake.

The former of these approaches most nearly the eutrophic type of Thienemann with low transparency, absence or great reduction of oxygen at the bottom in late summer and early autumn, rather high plancton productivity, and presence of Corethra. But Tanytarsus, which is characteristic of the oligotrophic type, is also present in Mendota. Green Lake, on the other hand, appears to conform more nearly to the oligotrophic type, being relatively deep, with a moderate amount of plancton, and oxygen present at all depths, though much reduced at the bottom in late summer and early autumn. In comparison with Flathead Lake, Mendota shows much larger amounts of plancton and Green Lake considerably less, except in the case of the Entomostraca, which are somewhat more numerous in the latter.

We turn now to a brief consideration of a distinctly eutrophic type of lake, Devils Lake, North Dakota. This is a shallow lake whose level fluctuates considerably from year to year, but which, in 1920, had a maximum depth of approximately 6 m., while at the place where the work was done the depth was between 4 and 5 m. It is a highly alkaline lake with a total solid content in 1923 of 15,210 ppm. The bottom is covered with a layer of decaying ooze. The water is kept in more or less constant circulation by the wind, but in winter, when the lake is ice-bound, and after a few still, hot days in summer the oxygen in the bottom water is greatly reduced or entirely absent. There is an abundant growth of Ruppia and Cladophora in much of the lake. The great number of rotifers and Crustacea is clearly shown in Table 12.

I have been able to find very few data for foreign lakes which are in any way comparable to our own for Flathead Lake. The most extensive which I have found are those of Robert (1919) for Lake Neuchatel, which are given in Table 12. This is one of the larger, lower alpine lakes, which conforms to the oligotrophic type of Thienemann, and which resembles Flathead Lake in its general features rather closely. Bearing in mind the fact that the collections of Fuhrmann and Robert, upon which the latter's figures are based, were made with nets, while mine were made with the trap, which gives considerably larger amounts than the net, the results of the former collections and my own are not greatly different. Some collections from Neuchatel give larger amounts than those at similar seasons from Flathead Lake and vice versa, but in no case do the former approach in amount the collections from the latter made from April to June in 1929.

On the other hand, some of the figures given by Thienemann (1925, p. 186) for the Baltic lakes surpass any of those for Flathead Lake. Thus on March 21, 1924, there were 200,000 Stephanodiscus pr. cc. in the Eutin Lake, and on July 27, 1924 in the Pinn Lake Dictyosphaerium reached the enormous number of 700,000 cells pr. cc. But, as Thienemann says, these cases are exceptional. According to this author, in the Eifel region of Germany the deep lakes of the sub-Alpine type never show a higher plancton concentration than 1000 "individuen" pr. 1., while those of the shallow (Baltic type) may reach a concentration, even beneath the ice, of more than 100,000 pr. 1.

In the Swiss Lake of Brienz, which Flück (1927, p. 50) considers "der am dünnsten bevolkerte aller Alpenrandseen", he never found over 1800 "individuen" pr. 1. According to this author, "Bachmann gibt für den Vierwaldstattersee einen Wert von ca. 8000 Individuen pro liter." This was in November, which is not the period of maximum production in the latter lake.

Flück's figures are for the nannoplancton, obtained by centrifuging. Compared with these latter figures, those which I have given above for Flathead Lake are very high, with a maximum of over 400,000 cells (66,800 colonies) of Asterionella pr. 1. at Station 8 on July 2, 1929, and 395,000 cells (49,600 colonies) at Station 1 on April 16, 1929, and a maximum of 312,500 cells pr. 1. for Fragilaria at Station 1 on November 28, 1929.

This summary brings out clearly the relation between plancton abundance and the physico-chemical character of different lakes, and supports the contention of Thienemann (*l.c.*), Klugh (1926) and others, that the shallow type of lake with abundant vegetation is also the type with abundant plancton.

How do these lakes compare with each other in respect to the amount of their bottom fauna? Thienemann gives no adequate comparison between the bottom faunas of oligotrophic and eutrophic lakes due to lack of data for the former. Kemmerer et al. (*l.c.*) give no data for the northwestern lakes investigated by them, while the data for the Finger Lakes studied by Birge and Juday (*l.c.*, 1914) are admittedly inadequate. Muttkowski (*l.c.*) gives a table showing the distribution of 97 species[38] in Lake Mendota from the shore to a depth of 7 m., based on collections from 50 stations at each of the following depths: 0-1 m., 1-2 m., 2-3 m., 3-5 m., and 5-7 m., and Juday (1922) has given further data on the bottom fauna of this lake; while Birge and Juday (1921) have given a few data on that of Green Lake, Wisconsin, and Canandaigua, Cayuga and Seneca Lakes in New York.

Adamstone (1924) has made an extensive study of the bottom fauna of Lake Nipigon covering the years 1921-23, but during a few weeks in summer only. He also, in the same paper, gives a brief account of one series of dredgings in Lake Ontario.

[38] And 5 families of Hydracarina and an indeterminate number of leeches.

The bottom faunas of Lake Simcoe, Ontario, and Shakespeare Island Lake, situated in an island in Lake Nipigon, have been studied by Rawson (1928) and Cronk (*l.c.*) respectively. The latter is a shallow lake (12 m.) while the former is similar to Nipigon in its general features. The number of bottom animals in the latter (1568 pr. m.) is about double that in the former, while Nipigon is intermediate between them in this respect.

Eggleton (1931) has made a very thorough study of the bottom fauna of a small lake (Third Sister Lake) near Ann Arbor, Michigan, and a partial study of Douglas Lake in northern Michigan, together with some observations on Kirkville Green Lake near Syracuse, New York. The first of these is clearly of the eutrophic type with an abundant bottom fauna, while the last is a very peculiar lake, which, according to the author, is related on the one hand to the oligotrophic and on the other to the dystrophic lakes. It apparently belongs in none of the three types, but perhaps approaches the last most nearly.

Another recent investigation of interest is that of Scott *et al.* (1928) on Lake Wawasee in Northern Indiana, included in the drainage basin of Lake Michigan. It has an area of about 4,000 sq. km. and a maximum depth of 23 m. So far as I can judge from the data given, it is of the eutrophic type.

Lundbeck (1926) has given data for many north German lakes, including both eutrophic and oligotrophic types, while an extensive examination of a number of Japanese lakes, of both oligo- and eutrophic types, has recently been made by Myadi (1931, 1932) and Myadi and Hazama (1932), from which I have selected two (Motosu and Yogo) for comparison.

A comparison of the amount and general character of the bottom faunas of many of these lakes with that of Flathead Lake is given in Table 13. Because of the different dates and depths of the collections, such a comparison can be of general value only. By comparing collections of approximately similar seasons and depths for the different lakes, however, we can obtain a fair comparison of their bottom productivity.

A study of fresh water lakes shows that the underlying factor determining the abundance of life in lake as on land is food. The ultimate source of the food of aquatic and terrestrial organisms is the same—namely, the chemical elements dissolved in water; although in the case of terrestrial life, the air contributes a large part of the necessary carbon and oxygen. The chemical elements in the lake or river are in turn derived from rain water, which leaches the soil of their drainage basins. In the case of the lake, much of the food of the unicellular life—bacteria, algae and Protozoa—is derived from the larger vegetation, which flourishes best in shallow water; so that the depth of the lake, as Klugh (1926) has said, is perhaps the most important factor in determining the abundance of its life. Such a principle, of course, has its limitations. It is not to be expected that a hot spring, or a shallow pool at the base of a glacier, which is free from ice for only a few weeks

TABLE 13. Comparative abundance and depth distribution of the bottom fauna of 14 lakes in number of animals per square meter.

Lake	Depth in Meters	Turbellaria	Nematoda [30]	Oligochaeta	Hirudinea	Crustacea	Chironomidae	Culicidae	Total Insects [40]	Hydrachnida	Sphaeridae	Gastropoda	Total Molluscs	Total Fauna
FLATHEAD	1–3	3	....	....	3	61	43	....	83	3	54	51	105	258
	6–10	4[32]	....	53+4[33]	11	119	758+2[33]	....	794	25	169	32	201	1207
	14–18	....	3	38+3[33]	9	....	423+6[33]	....	423	9	25	6	31	513
	23–36	2	25—27[32]	27+7[32-33]	....	....	171+4[32-33]	....	171	7	11	....	11	243
	49–55	8	96	....	....	....	96	....	96	....	....	....	....	200
	83–94	....	632	28	....	....	56+12[33]	....	56	....	4	....	4	720
	Average[31-39]	3	97	29	8	95	308	....	323	12	60	30	78	645
CANANDAIGUA	20	....	....	1420	....	977	....	....	800	....	....	....	....	3197
	74	....	....	890	....	844	....	....	45	....	....	....	....	1779
	Average	....	....	1155	....	910	....	....	422	....	....	....	....	2487
CAYUGA	34	....	....	....	....	178	....	....	133	....	....	....	....	311
	113	....	....	1288	....	710	....	....	3863	....	....	....	....	5861
	Average	....	....	644	....	444	....	....	1998	....	....	....	....	3086
SENECA	32	....	....	5240	....	1110	....	....	89	....	....	....	....	6439
	47	....	....	1330	....	844	....	....	577	....	....	....	....	2751
	110–172	....	....	843	....	244	....	....	244	....	....	....	....	1331
	Average[39]	....	....	2064	....	610	....	....	288	....	....	....	....	2962
GREEN	45	....	....	1480	....	6882	....	....	74	....	....	....	....	8436
	66	....	....	1643	....	459	....	....	407	....	....	....	....	2509
	Average	....	....	1561	....	3670	....	....	240	....	....	....	....	5471
ONTARIO	12	..	....	192	....	16	....	....	576	....	....	....	1856	2640
	31	....	16	2512[42]	....	32	....	....	288	....	....	....	176	3024
	54	..	32	368	....	448	....	..	16	....	....	....	192	1056
	85–93	....	104	64	....	440	....	....	8	....	....	....	128	744
	113–125	....	48	8	...	40	....	....	....	....	..	....	8	104
	Average[39-41]	....	50	459	....	208	....	...	224	....	....	....	393	1334
WAWASEE	3	14	....	10	28	1157	169	2	300	....	7	243	250	1759
	5–9	2	....	5	9	125	223	9	296	....	88	91	179	616
	11–19	....	....	32	1	....	740	185	939	....	157	8	165	1137
	21–23	..	....	....	....	...	332	258	590	....	77	....	77	667
	Average[39-41]	4	....	21	8	307	473	135	642	....	110	62	172	1154
THIRD SISTER	5–10	....	....	4323	....	....	2219	853	3072	247	....	....	....	8124
	11.5–15	....	....	7731	....	....	1007	8923	9930	49	....	....	....	17743
	16–18	....	....	577	....	...	274	25604	25878	15	..	...	...	26472
	Average[39-43]	...	....	4136	....	....	1308	10324	11632	127	....	....	....	16126
MENDOTA	0–3	....	1	367	5	114	119	....	330	75	....	....	137	1029
	3–7	....	....	1090	7	184	120	5	179	48	....	....	299	1807
	Average[39-41]		1	656	6	142	120	2	269	64	....	....	202	1340

TABLE 13. *Continued*

Lake	Depth in Meters	Turbellaria	Nematoda [39]	Oligochaeta	Hirudinea	Crustacea	Chironomidae	Culicidae	Total Insects [40]	Hydrachnida	Sphaeridae	Gastropoda	Total Mollusca	Total Fauna
NIPIGON	0–30	....	....	86	....	118	517	.....	576	....	....	...	274	1054
	30–60	....	....	36	....	224	183	.....	188	....	....	...	82	530
	60–90	....	....	19	....	402	103	....	103	....	....	....	20	544
	90–150	...	....	56	....	905	59	....	60	...	....	...	26	1047
	150–210	....	....	60	....	726	139	....	140	....	....	....	7	933
	210–390	....	....	218	....	1078	84	.....	84	....	..	....	27	1407
	Average[39]	....	....	129	....	806	131	.....	136	....	....	...	46	1117
MADU	Average	....	....	1665	...	...	157	....	157	....	151	....	151	1973
GREATER LAKE OF PLON	Average	....	....	305	....	....	171	.....	171	....	68	....	68	544
MOTOSU	23–38	.. .	....	227	6	....	422	....	422	....	....	....	6	661
	40–60	10	....	104	....	....	114	....	114	....	....	....	....	228
	66–89	....	10	187	....	42	83	....	83	....	52	....	52	374
	97–119	3	....	208	....	28	184	...	184	....	15	....	15	438
	Average [39-41]	3	3	194	6	19	212	.....	212	....	15	....	17	448
YOGO	0–3	....	....	23	....	....	19	.....	20	....	....	....	164	207
	3–6	....	....	53	....	....	102	1	104	....	...	...	100	257
	6–10	....	....	179	....	....	174	306	485	....	....	....	18	682
	10–13.5	....	. ...	415	....	....	82	1638	1720	....	....	....	....	2135
	Average[39-41]	....	....	201	....	....	112	592	706	....	....	....	70	977

in summer, will furnish an abundance of life equal to that of a temperate lake. But, other things being equal, and within reasonable limits, the law holds good that the deeper the lake the less the average amount of life which it contains.

Closely allied with depth and largely dependent thereon is temperature. Within certain limits the higher the average temperature of a lake and the longer its summer season, the greater will be its productivity. As we have already seen,* however, the periods of maximum plancton abundance do not, in general, coincide with the warmest season, and especially is this true in the case of diatoms, which have their maximum development in Flathead Lake in May, when the temperature ranges from 4° to 8°. Other investigators

[39] Averages based on all collections taken separately, some of which have been combined in the tabulation, as indicated in the depth column.
[40] Includes a number of forms besides those listed in the table.
[41] Averages based on maximum depth given in table for each species.
[42] "The remainder of the material was left overnight, with the result that a great many Oligochaeta disintegrated." (Adamstone, 1924).
[43] The averages for Third Sister Lake include a number of forms listed by Eggleton as "all others", and not included in this table.
* See page 120 *et seq.*

have noted the same relation, although in general their temperatures are somewhat higher than these.[44]

Eggleton (*l.c.*) has shown also that the maximum production of benthos in Third Sister Lake, Michigan occurs in winter, and the minimum production in late summer or early autumn. There are so many factors involved in determining the amount of life in a lake that to attempt to relate it exclusively to one of these is an absurdity.

Steuer (1910, p. 606) points out that the lakes of northern Germany and, in part, of Norway have a much greater plancton productivity than do those of the Alps, of Istria or of the Balkans; apparently overlooking the fact, however, that the character of the lake itself determines its productivity and that latitude, in itself, has nothing to do with it. Furthermore, it is impossible at present to make any satisfactory comparison of the productivity of different lakes because of the different methods of investigation employed by various workers,* and because very few lakes have been studied thoroughly enough to give an adequate idea of what their productivity really is.

Not only in respect to amount of plancton and benthos, but of littoral vegetation as well, Flathead Lake belongs in the class of oligotrophic or poor-productive lakes; although it is by no means an extreme example of this class, having a much greater productivity than many mountain lakes in both Europe and America as, for example, the Lake of Brienz in Switzerland or Tahoe, Crater and Chelan in America. In point of productivity it corresponds more nearly to Lundbeck's (*l.c.*) type Al,* which is characterized by a Tanytarsus-Chironomus society and is represented by the Madü and Dratzig lakes of northern Germany and Lake Lugano in the Italian Alps.

In respect to the character of the life of any region, the determining factors are widely different in water and on land. In the first place, climatic changes on land are much greater and more sudden than in water. A priori one might expect that warm-blooded animals, like birds and mammals, would be less dependent on the temperature of their environment than cold-blooded types. And to a certain extent this is true, for reptiles are characteristically tropical, while birds and mammals range throughout all latitudes. But the factor of food, which is closely correlated with that of temperature, enters here, as does that of the rearing of young also.

Natural waters, as contrasted with air, show much smaller range of temperature. The lower limit is about 0° while the upper limit, in any lake of considerable size or depth, is seldom more than 25°, while changes take place gradually in water, so that its life is not subject to the vicissitudes of terrestrial or aerial forms.

That aquatic organisms are profoundly influenced by temperature is easily seen by comparing the life of the Labrador current with that of the

[44] Wesenberg-Lund (*l.c.*)
* See page 116.

Gulf stream, or the life of a cold mountain brook or lake, at the head waters of a river, with that of the sluggish streams and warmer lakes near its mouth. Ciscoes (*Leucichthys artedi*) are common in Green Lake, Wisconsin, but rare in Lake Mendota, while just the opposite distribution is characteristic of the yellow perch (*Perca flavescens*), a difference related by Pearse (1921) primarily to temperature. And Cahn (1927) has shown the sensitivity of the cisco to temperatures above 17° by tank experiments. In the case of fresh water life, however, so many factors enter into its environment that it is even more difficult than with land animals to determine the part played by temperature in determining its distribution.

One of the most important of these factors is the chemistry of the water. While terrestrial plants are directly affected by the chemical character of their environment (i.e. soil) the animals are, in the main, only indirectly so affected through the character of the plants upon which they feed. In water, however, both plants and animals are directly influenced by its chemical character, changes in which may produce corresponding changes in the life which it contains. Perhaps nowhere are these changes better exemplified than in Devils Lake, North Dakota, for here, in less than the span of a human life, a lake has changed so greatly in its salt content as to profoundly influence the life which it contains.

"Devils Lake is one of many lakes in the western United States, which, through lack of inlet and excess of evaporation over precipitation, is gradually drying up and steadily increasing in salt content and alkalinity. (Chemical analyses) show an increase in salt concentration, accompanying the decrease in lake level, from 8471 ppm. in 1899 to 15,210 in 1923. According to early settlers in the region, it formerly swarmed with pickerel and, until recently, the stickleback (Eucalia inconstans) was very abundant there. Lord (1884) reported a few 'shiners' and Pope (1908) stated that the minnow (Pimephales promelas) was abundant in 1907. No minnows have ever been found by me in the lake and the sticklebacks, which until 1915 were fairly common, are now much less numerous than formerly." (Young 1924, p. 28). This concentration has resulted in the exclusion of many types which are ordinarily common in fresh water—Gastropoda, Sphaeridae, Bryozoa, Macrura, Branchiura, Oligochaeta, Hirudinea, Hydrozoa and Porifera. Of these, gastropods must formerly have been numerous in the lake, as their shells have been found about the shore in recent years.

During the work of Young (*l.c.*) at the lake from 1909 to 1923, the rotifer *Triarthra longiseta* apparently disappeared, with concentration of the water above 1%, being present sparingly from 1909 to 1912 but not seen subsequently to the latter date in the lake proper; although in one of its bays, which, due to high water in 1916 was much reduced in salinity, it was reported by the late Mr. Harry K. Harring in two collections as "abundant" and "common".

In chemical character the water of Flathead Lake is in no way peculiar unless it be for its great purity, which is probably mainly responsible for the comparative paucity of its plancton and benthos. The pH values (8.21 to 8.63) show that the water is distinctly alkaline, as would be expected from the geological nature of its watershed, but I am unable to find in the character of its biota any distinct effect of this alkalinity. Mr. F. J. Myers, however, who has identified the rotifers, writes that the "collections as a whole indicate an alkaline . . . fauna . . . with the acid water species almost wanting".

In this connection the rarity of Brachionus is of interest. We have only one record, from the old outlet of the Flathead River (8/1/28). It is also of interest to note that Kemmerer *et al.* (1923), in a reconnaissance of 49 lakes in California, Oregon, Washington and Idaho, report Brachionus from one only, Medical Lake, Washington, a lake of low oxygen content and high alkalinity, and in which, according to these authors "Rotifera were especially abundant at all depths" (*l.c.*, p. 89). Furthermore, in his study of the plancton of Lake Nipigon, Bigelow (1923, p. 53) reports that "only one specimen of (Brachionus) was found during the season . . . in a small pond . . ." but not in Lake Nipigon itself. According to Harring and Myers (1928) the pH value of any water is one of the determining factors in rotifer distribution, and Haempel (1926) has emphasized the importance of this factor in determining the life of a lake. Myers (1931) lists Brachionus as a "typical alkaline-water" genus. Kemmerer et al. (*l.c.*) give no pH values for the lakes studied by them, but list several as "hard" some as "medium" and others as "soft" water lakes with respect to the amount of "fixed CO_2 content". McKay (1924) gives pH values of 7.9 to 8.4 for Lake Nipigon water, thus classifying it as a distinctly alkaline lake. Whatever may be the reason for the scarcity of Brachionus in Flathead Lake and other waters where it might be expected to occur, "there are unquestionably other factors",[45] than simply pH value involved. A similar conclusion has been reached by Behrens (1933) regarding the distribution of rotifers in the pools of East Holstein.

In Flathead Lake "The desmids, both from the standpoint of number of species and actual numbers of individuals, made up the most important part of the green algae. More species (91, representing 23 genera) and a greater number of individuals were found than all the rest of the green algae combined. They were found almost entirely in the shallow bays but occasionally a few individuals were picked up in the plancton trap. The greatest numbers of these forms were found in Hell-Roaring Bay and the mouth of the Swan River. Very few were ever found at any of the other places of collection."[29]

Wesenberg-Lund (1908) ascribes the abundance of desmids in the Irish and Scotch lakes to drainage from peat bogs or mossy mountain banks. While the number of species in these lakes is large, the number of individu-

[45] Harring and Myers (*l.c.* *p.* 675).

als is small. The Wests (1909) ascribe the abundance of desmids in the Scottish lakes to the geological formations of this region, which are older than the Carboniferous, and which fact Pearsall (1921) relates to the high ratio of sodium and potassium to calcium and magnesium in the water; while West and Fritsch (1927) ascribe their abundance to the humic acid in the water, but Murray (1905) questions this interpretation because of their abundance in the clear waters of Loch Morar and their scarcity in the brown waters of Loch Ness. It is unlikely that the age of the geological formation of any water has in itself any necessary relation to the life of that water. The chemical character of the rocks, however, undoubtedly has a very important relation thereto, through its influence on the water.

In Flathead Lake neither sodium and potassium which are much less in amount than calcium and magnesium, nor abundant rainfall, leaching humic acid out of a heavy carpet of mosses, are adequate to explain the variety of desmids there present. Here again we meet with one of those perplexing problems which are at the same time the despair and the delight of the limnologist.

A third factor which affects terrestrial and aquatic organisms differently is barriers. Excepting flying forms, such as birds and bats, and to a less extent insects, the distribution of terrestrial life is profoundly influenced by barriers. In many cases they doubtless play the major rôle in determining its distribution. With most aquatic life, however, the case is different. In whatever way these forms may be spread, whether in feathers of birds or fur of mammals, by flood or by winds, the fact remains that, excepting fish, they are much more widespread in their distribution than are most terrestrial forms, a large number of them, indeed, being cosmopolitan.

In his extensive comparison of the plancton of the lakes of the world, Wesenberg-Lund (*l.c.*) emphasizes its cosmopolitanism. He says (p. 313): "The fresh water plancton is characterized by its well-marked cosmopolitanism. Against this it can at most be said that in the high-arctic zone some types are apparently absent, that the great African lakes are characterized by their remarkable Diatom plankton and that some few genera and species (*Sida limnetica, Limnosida frontosa*) are restricted to rather limited areas; only the Diaptomidae, according to our present classification and knowledge, seem to have a distribution which is fairly sharply delimited for each species.

It must be emphasized that the fresh water plancton communities, in contrast to all other communities on land or water, everywhere contain the same types, nearly everywhere the same species. The Arctic or North European zone and the tropical zone have a very large number of species is common. This applies especially to the Diatoms, Cyanophyceae, Chlorophyceae and Flagellata; further amongst the Rotifera: *Anuraea aculeata, Polyarthra platyptera, Asplanchna Brightwelli, Triarthra longiseta,* species of the genus Brachionus, Pedalion; amongst the Cladocera: *Bosmina longirostris* and *core-*

goni, Ceriodaphnia cornuta, Daphnia hyalina, Chydorus sphaericus; amongst the Copepoda: *Cyclops serrulatus, C. Leuckarti, oithonoides,* etc. In no other community is so great a number of species common to the whole world, only very few new types are found on comparing the plancton of northern latitudes with that of southern. Considering to what a degree the different plant and animal communities, terrestrial as well as marine, change from the pole to the equator, how no end of new types appear for every degree of latitude as we proceed to the south, the cosmopolitanism of the freshwater plankton must first and chiefly be emphasized as its greatest peculiarity and one of its greatest puzzles, which we are at present unable to solve with certainty. . . .

Compared with this phenomenon the supposed maintenance of sharply delimited areas of distribution for certain fixed genera and species is of quite secondary importance. If we try by means of such areas, which appear at present apparently natural and well-defined for some species within certain groups of animals, to divide the fresh water plancton into similar well-marked zoö- and phytogeographical territories like those of other communities, we find that the attempt quite fails."

Bachmann (1924), on the contrary, stresses the individuality of lakes as follows (p. 28): "Schon Forel hat darauf hingewiesen, dass jeder See einen Organismus für sich darstelle. Und alle die Monographien der Schweizer seen, . . . stimmen darin überein, dass, wie ich schon früher bemerkt habe, nicht zwei Seen . . . mit einander in ihrem Pflanzenbilde identisch sind."

These two views are, however, by no means contradictory. True it is that the plancton, as a whole, *is* cosmopolitan. But it is also true that every lake and pond has its own peculiarities in physical and chemical conditions, which in turn determine its life, so that the latter is as variable as the former; and any attempt, such as that of Dodds (1920 *et al.*) whch seeks to bring the distribution of aquatic, into line with that of terrestrial life on the basis of one factor, i.e. altitude (temperature), but fails to consider the manifold other factors in the environment, is wholly inadequate to explain such distribution.

If we compare the life of the oligotrophic lakes of North America and Europe, we find in one the diatoms predominant among the algae, in another the blue-green, and in another the green algae. In one lake desmids are common, in another rare. In one lake Diaptomus is the principal copepod, in another Cyclops, and in yet another Epischura. There is one group, however, certain members of which are practically universal in their distribution—the "cosmopolitan group of rotifers" of Wesenberg-Lund (*l.c.*). That lake is indeed exceptional in which Anuraea, Notholea, Triarthra, Polyarthra and Asplanchna are not present.

That the life of Flathead Lake is not constant, but changing is apparent from the statement of Forbes (1893, p. 237) that "four-fifths to nine-tenths of the product of every deep-water haul with the surface net" was com-

posed of Daphnia thorata (longispina), whereas, at the present time, this form is far inferior in numbers to Cyclops and usually to Diaptomus. According to Forbes, also, Epischura was much commoner than Diaptomus, which latter "was not certainly seen at all in Flathead".[46]

A similar observation has been made by Eddy (1927) regarding the occurrence of Epischura lacustris in Lake Michigan, which, while common forty years ago, was lacking in recent collections. Eddy, however, found that in general the life of Lake Michigan today is the same as that of forty years ago. Marked changes in the plancton of the Red Lake, a small lake near Luzern, Switzerland, are also described by Bachmann (1931) ; and Wesenberg-Lund (*l.c.*, p. 293) says "Even in the twenty years during which I have studied the plancton in a few lakes, I believe I have seen forms die away and new arise".

Thienemann (1925, p. 179) also says "In anderen Seen stachen die Unterschiede noch greller hervor: der Schohsee erzeugte in Herbst 1921 eine Oscill, rubescens-Wasserblute; 1 Jahr später war dort kein Faden aufzufinden. Im Vierersee war das Tiefenwasser im Herbst 1921 rötlich gefärbt durch Thiorhodaceen. Im Jahre darauf konnte dort keine Zelle nachgewiesen werden; wohl aber waren Einsenbakterien an derselben Stelle vorhanden." Similar cases are cited by Minder (1926) for the Lake of Zurich and by Lundbeck (1926) for several North German lakes, and doubtless could be found in any lake which was studied for several years.

In the case of the Red Lake above cited, as in that of Devils Lake, North Dakota,* these changes are undoubtedly due to changes in the chemistry of the water, but in other cases no such explanation is available.

Regarding the origin of the life of Flathead Lake, but little can be said. Its vertebrates, apart from some introduced forms, are clearly part of the fauna of the western slope of North America, while its plants and invertebrates are, in general, species of wide distribution, indicating the effect of the Rocky Mountain barrier upon the former and the absence of such influence upon the latter.

SUMMARY

In this paper I have endeavored to set forth the composition of the life of Flathead Lake together with the factors of its physical environment, as representative of the many mountain lakes of western North America. My work indicates that the lake is of the oligotrophic type—a deep, pure, cold mountain lake with a correspondingly low productivity of plancton and benthos. Factors determining the character and distribution of the life of lakes are discussed and questions raised regarding their correlations and the origin of lake biotas in general.

LA JOLLA, Calif.

[46] In comparing our results with those of Forbes it should be noted that his collections were made in only one part of the lake, and on a single day, so that too much weight cannot be placed on the comparison.

* See page 154.

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THE BIOLOGY OF THE THATCHING ANT, *FORMICA RUFA OBSCURIPES* FOREL, IN NORTH DAKOTA

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CONTENTS

THE BIOLOGY OF THE THATCHING ANT, *FORMICA RUFA OBSCURIPES* FOREL, IN NORTH DAKOTA

I. INTRODUCTION

The thatching ant, *Formica rufa obscuripes* Forel, is widespread in North Dakota and lives in conspicuous thatched mounds. I have been able to find in the literature only one reference to it in North Dakota (McCook, 1884). Specimens of ants from nests at Jamestown were sent to Rev. McCook by R. G. DePuy, M.D. McCook called these *Formica rufa* and the description of the mounds leaves no doubt that they were *obscuripes.* DePuy's measurements show heights of mounds varying from eight inches to one and one-half feet and what was probably the brood chamber was occupied by "a ball of twigs, about eight inches in diameter." DePuy reports that there were never more than three openings, usually near the summit. He found chambers extending down as far as he dug, four and a half feet. Apparently his observations were made in the fall or early spring as the ground was already frozen.

McCook reports conversations with another resident, Mr. B. S. Russell, to the effect that numerous swarms of "flying ants" appear from late July into September and erroneously assumes that they were *obscuripes.* I have seen many swarms of winged ants which were much smaller than *obscuripes* and were of species of *Myrmica* and *Lasius.* Frequent inquiries of residents of the state have invariably brought the statement that the swarms of winged ants are the smaller ants which I have seen. A swarm of winged ants as large as the male and female *obscuripes* would be very conspicuous.

Mr. Russell also mentions the damage to the thatch mounds by prairie fires which "burn them quite up, and penetrate far enough beneath the surface to leave a hole that would contain a bushel-basket!" McCook states that the nests frequently are protected from prairie fires by "a narrow belt of smooth soil [which] generally surrounds the base of a hill, on the outer margin of which springs up a circle of tall, stiff, thick-stalked grass. . . ." "This grass remains green until late in the fall, and when the dry prairie is swept by the flames, it stands as a breastwork around about the mounds, often deflecting the fire or greatly modifying its destructive effects. In this way the formicaries are kept safe within the girdling ranks of the friendly plant." My studies do not bear out this statement. I have found several nests surrounded by dense grass which was encroaching upon the mounds. One of these nests had been burned by a prairie fire as shown by the charred twigs within the mound. It is more probable that these margins of grasses or herbs increase the danger from prairie fires.

McCook also states that the mounds are made of "an alternation of

layers of earth and vegetable substance, the latter falling into decay in due season." Such a structure is accidental and is not found in the average vigorous nest during normal years. Soil is brought up in excavating the chambers below but is carried either to the margin of the mound or dropped in such small amounts upon the nest as to be a negligible factor in nest structure. In very dry springs, however, such as that of 1934, an enormous amount of soil is transported by the frequent winds. Much of this wind-blown soil lodges in the thatch.

This brief and none too accurate account by McCook constitutes practically all which has been published on the ant fauna of the state.

The following observations were made chiefly in McHenry County which is situated in the north central part of North Dakota, about equidistant from the Montana and Minnesota state lines and twenty-five miles from the Canadian boundary. The physiographic and biological characteristics of this county are fairly representative of the state.

This paper is a condensed and revised form of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at the University of North Dakota. To Professor G. C. Wheeler, under whom this study was undertaken, I wish to express my sincere appreciation of his generous assistance. I am also indebted to Dr. E. A. Baird, Professor of Botany at the University of North Dakota, for aid in the determination of plants and to Professor W. M. Wheeler of Harvard University and Dr. Esther W. Wheeler for helpful suggestions.

II. DISTRIBUTION

Formica obscuripes is an ant of western North America. Since *aggerans* is a synonym of *obscuripes* and since the status of the variety *melanotica* is doubtful, their distribution will be given together. Wheeler (1913 and 1917) records this ant from the following states and provinces:

Wisconsin	Montana	Idaho	Manitoba
Illinois	Wyoming	Utah	Alberta
North Dakota	Colorado	Arizona	British Columbia
South Dakota	New Mexico	Oregon	Washington
Nebraska	Texas	California	

Recently it has been collected in Minnesota at Delorme, Erskine and Little Falls by G. C. Wheeler and at Mallory, Walker and Bemidji by myself. I have seen specimens in the United States National Museum from Iowa and have collected *obscuripes* at Gainsborough, Saskatchewan.

F. obscuripes is found in North Dakota from the Red River "Valley", forming the eastern boundary, to the Badlands near the western boundary. It ranges in altitude from the lowest part, the Red River "Valley", at an

elevation of about 800 feet (244 m.) to the very highest point in the state, Black Butte, at an elevation of 3468 feet (1077.7 m.).

It has been collected from the following localities in North Dakota, the collectors' initials G. C. W. and N. A. W. representing G. C. Wheeler and myself:

Walhalla (G. C. W.)	Pembina County
Niagara, Larimore (C. V. Johnson), Grand Forks and Arvilla (N. A. W., G. C. W.)	Grand Forks County
Binford (M. A. Hetland)	Griggs County
McHenry (M. A. Hetland)	Foster County
Jamestown (H. C. McCook)	Stutsman County
Leeds (N. A. W.)	Benson County
Bottineau, Lake Metigoshe (N. A. W.)	Bottineau County
Balta, Barton, Rugby (N. A. W.)	Pierce County
Towner, Upham, Norwich, Granville, Denbigh, Guthrie, Bantry, Smoky Lake, Anamoose, Velva, Drake, Round Lake (N. A. W.)	McHenry County
Minot (N. A. W.)	Ward County
Sherwood (N. A. W.)	Renville County
Dunseith (N. A. W.)	Rolette County
Butte, Washburn (N. A. W.)	McLean County
Parshall, Plaza (N. A. W.)	Mountrail County
Bismark, Sterling (N. A. W.)	Burleigh County
Denhoff (N. A. W.)	Sheridan County
Hebron, Glen Ullin (Emil Krauth), Breien, Mandan (N. A. W.)	Morton County
Yucca (N. A. W.)	Oliver County
Sentinel Butte (G. C. W.), Trotters (J. E. Goldsberry)	Golden Valley County
Bicycle (G. C. W.)	McKenzie County
Medora (N. A. W., G. C. W.), Mikkelson (J. E. Goldsberry)	Billings County
Black Butte, Amidon (G. C. W.)	Slope County

Obscuripes is found throughout McHenry County, the ants avoiding only small unsuitable areas such as the damp borders of sloughs and the wooded Mouse River Valley.

III. TAXONOMY

The ant, *Formica rufa obscuripes* Forel, belongs to the family Formicidae in the order Hymenoptera.

Formica rufa was first described by Linné in the 10th edition of his *Systema Naturae*, Volume 1, p. 580, in 1758.

The subspecies *obscuripes* was first described by Forel in 1886 (Ann. Soc. Ent. Belg. 30, C. R. p. 39) from specimens collected at Green River, Wyoming. Only the workers were described and these so inadequately that Wheeler (1912, p. 90) named the same ant *Formica rufa aggerans*. Later

(1913, p. 430) he fully described the castes of *aggerans* and (pp. 433-434) redescribed *obscuripes* suggesting that further study may show them to be the same subspecies. In 1917 (1917, pp. 535-537) Dr. Wheeler definitely cleared up this question of nomenclature by synonymizing *aggerans*. Previous to this many observers had reported *obscuripes* under the name of *aggerans* from a wide area in the western part of the United States.

Forel's original description of *obscuripes* is as follows:

Ouvrière. Long., 3, 8 à 8 mill. Très semblable à la *F. rufa i. spec.* d'Europe. Mais elle est plus petite; les grandes ouvrières sont d'un rouge plus clair et presque ou entièrement sans tache sur la tête et le thorax, tandis que les pattes et l'écaille sont d'un brun noirâtre. Les petites ouvrières sont beacoup plus foncées et tachées de brun sur la tête et le thorax. L'abdomen est mat, noir, et a une pubescence grise un peu plus forte que chez la *F. rufa i. sp.*, tandis que la pilosité est plutôt un peu plus faible.—Green River, Wyoming (Scudder).

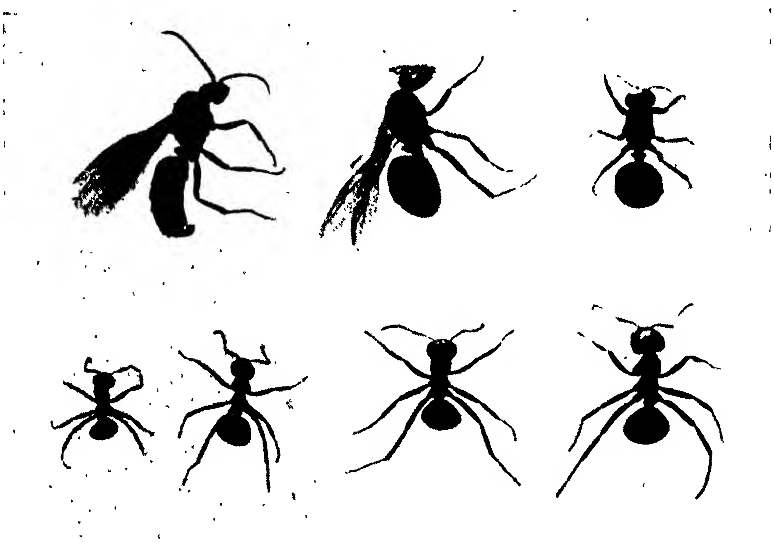

FIG. 1. *Formica rufa obscuripes* Forel. Above: winged male, winged female, queen. Below: minima, media, and maxima workers.

Emery in 1893 (Zool. Jahrb. Syst. Vol. 7, p. 650) established the variety *melanotica* as a form of *obscuriventris*:

Einige ☿ aus Wisconsin sind noch dunkler rostbraun mit mehr blutrothem Kopf.

In 1910 Wheeler (p. 570) regarded it as a variety of *obscuripes,* but in his monograph of the genus *Formica* (1913, p. 432) he transferred it to the subspecies *aggerans* and described the castes.

Representative ants from typical nests from widely separated localities in the state were sent to Dr. W. M. Wheeler in March 1932. These were all thought to be the variety *melanotica* because *obscuripes* was considered a form restricted to the Rocky Mountains and westward. Of these representative specimens Dr. Wheeler wrote, "I . . . should pronounce them all to be specimens of *Formica obscuripes* Forel. There are some color differences and perhaps the very darkest ought to be designated as Emery's variety *melanotica,* which in the large worker has the thorax black and only the head red. I am wondering, however, whether this variety has any validity, since there is such a variation in the same colony from dark minima worker up to maxima forms with rather light red head and thorax."

From my observations in North Dakota I would concur in this opinion that *melanotica* as a variety of *obscuripes* is of doubtful validity, for the following reasons:

1. Some workers from a colony may answer the description of *obscuripes* perfectly, while others of the same size from the same colony may equally well fit the description of *melanotica.*
2. Workers from one colony may answer the description of *obscuripes* while workers of the same size from a similar nest nearby may answer the description of *melanotica.*
3. All gradations of color from completely dark brown or black minima workers up to maxima workers with orange red heads and thoraces may be present in the same colony.
4. Such color differences as occur are not correlated with nest structure or habitat.

IV. ENVIRONMENT

A. Physiographic Conditions

1. North Dakota:

North Dakota includes parts of two great physiographic regions of North America, the Central Lowland and the Great Plains. The Missouri River forms the boundary between the two. For a complete account of the physiography of the state see Leonard (1919).

2. McHenry County:

McHenry County lies almost entirely in the Drift Plain of the Central Lowland, but with the Missouri Plateau crossing the southwestern corner. In general the surface of the county is gently rolling. The most striking features are the small hummocky sandhills or sand dunes which cover considerable areas, especially north, west, and south of Towner. These hills are 10 to 30 feet (3-9 m.) high and sometimes occur in irregular ranges. They are of pure sand and the tendency of the prevailing northwesterly winds is to give them a long windward slope and a sharper leeward slope.

Naturally, the binding effect of vegetation is to modify and resist the migration of these hills; but, where the cover of vegetation is scanty, the hills are true migrating sand dunes. There are a few scattered hills, as Buffalo Lodge near Granville and White Rock near Denbigh which are higher morainic hills. The rough belt of the hills of the Altamount Moraine crosses the southwestern corner.

There are no elevations in the county higher than 1800 feet (548.6 m.) above sea level, most of the county lying between 1400 and 1500 feet (426.7 m. and 457.2 m.).

The county is incompletely drained by the Mouse (or Souris) River and its tributaries, Wintering, Deep, and Little Deep "Rivers" and a number of small intermittent creeks. There are a number of small lakes, especially in the southern part, and many sloughs. Most of the lakes are "alkaline", which dry up during drouth years, leaving barren, salt incrusted, white "alkali" flats.

B. METEOROLOGIC CONDITION

1. NORTH DAKOTA:

North Dakota, situated as it is in the center of North America, has a truly continental climate. Temperatures in the summer of 100°F. (38°C.) to 105°F. (40.6°C.) are common and in the winter temperatures of —20°F. to —30°F. (—23°C. to —34°C.) are frequent.

The average annual rainfall for the state is slightly over 17 inches (43 cm.) and varies from 12 to 22 inches (30 cm. to 56 cm.) per year. The eastern half of the state has the highest rainfall, the Red River "Valley" being generally the wettest area. The western part of the state is the driest, averaging 10 to 15 inches (25 cm. to 38 cm.) per year. Rain falls mostly in the spring and summer months. Snowfall is light, being heaviest in the Red River "Valley" and decreasing westward. In the western part of the state the ground is frequently bare of snow in the winter for weeks at a time.

The winds are prevailingly northwestern. Winds from some direction occur most days of the year and in the spring are apt to be in the nature of violent sand or dust storms.

B. MCHENRY COUNTY:

McHenry County has a climate perhaps more rigorous than most counties of the state. Climatological data from the United States Weather Bureau records for Towner are typical for the county as a whole, since there are no complications due to appreciable differences in altitude, exposure, or other factors.

Maxima of 105°F. (41°C.) are not unusual and 108°F. (42.2°C.) has been recorded. Minima of —30°F. (—34°C.) in the winter are not infrequent, —49°F. (—45°C.) being the lowest recorded. Temperatures of

32°F. (0°C.) have been recorded every month of the year but infrequently in July. The ground generally freezes to a depth of 6 to 7 feet (180-215 cm.)

The average annual rainfall over a period of 30 years is 15.7 inches (40 cm.), the maximum being 28.7 inches (72.9 cm.) and the minimum 8 inches (20.3 cm.) per year. Seventy-eight per cent of the rainfall falls in the months from April to September inclusive. Snowfall is very light, the prairie generally having a very scanty covering or none at all. Snow generally forms drifts in sheltered places.

Winds are prevailing northwestern, winds from some direction occurring most days of the year.

C. PLANTS AS A FACTOR OF THE ENVIRONMENT

1. NORTH DAKOTA:

The vegetation of North Dakota is relatively homogeneous over the state and a clear, distinct geographical classification cannot be made. There is considerable overlapping of the different plant regions and in most places they are not sharply defined. The woodlands bordering rivers may straggle out on the prairie, particularly following up valleys. The prairie may border rivers as in the northern part of McHenry County along the Mouse River. Since altitude in itself does not exert a conspicuous effect upon the flora there are not the better defined plant zones of many regions.

For the plants of the state and their distribution reference may be made to Bergman (1912).

2. MCHENRY COUNTY:

The flora of McHenry County may be more readily classified since only a small area is considered. The flora may be divided into:

(1). MOUSE RIVER VALLEY. The valley is forested by the same deciduous trees characterizing the rest of the state, the ash (*Fraxinus pennsylvanica* Marsh.), oak (*Quercus macrocarpa* L.), box elder (*Acer negundo* L.), elm (*Ulmus americana* L.), willow (*Salix* spp.), and, in addition, dense pure stands of the quaking aspen (*Populus tremuloides* Michx.). Characteristic shrubs which I have collected are:

Betula glandulosa Michx.
Prunus americana Marsh.
Prunus virginiana (L.)
Ribes oxycanthoides L.
Amelanchier alnifolia Nutt.
Cornus stolonifera Michx.
Viburnum pubescens (Ait.)
Viburnum opulus L.
Salix discolor Muhl.
Salix longifolia Muhl?
Crataegus chrysocarpa Ashe

Herbaceous plants collected include:

Bidens cernua L.
Epilobium adenocaulum Haussk.
Helianthus maximiliani Schrad.
Helianthus autumnale L.
Helenium autumnale L.
Oxalis cymosa Small.

Mentha arvensis canadensis L.
Asclepias incarnata L.
Equisetum laevigatum R. Br.
Carex siccata Dewey?
Thalictrum occidentale A. Gray.
Vernonia fasciculata Michx.

(2). PRAIRIE. McHenry County lies in the transition between the short grass and long grass prairie and the plants would thus be somewhat representative of the state. In addition to the plants listed by Bergman for the state as a whole and characteristic of the prairie, other plants, which I have collected from the upland prairie, include:

Grasses:

Stipa comata Trin. and Rupr.
Bouteloua gracilis Lag.
Calamagrostis hyperborea Lang.
Agrostis hyemalis (Walt.) BSP.
Hordeum jubatum L.
Panicum capillare L.
Poa pratensis L.
Poa nemoralis L.
Poa compressa L.
Poa buckleyana Nash.?
Koeleria cristata (L.) Pers.
Calmovilfa longifolia (Hook) Scribn.
Andropogon furcatus Muhl.

Cacti:

Mammilaria vivipara (Nutt.) Haw.
Opuntia fragilis (Nutt.) Haw.

Herbs:

Lepachys columnaris (Sin.)
Chrysopsis villosa (Nutt.)
Solidago missouriensis Nutt.
Solidago rigida L.
Aster multiflorus Ait.
Artemesia canadensis Michx.
Artemesia caudata Michx.
Artemesia frigida Willd.
Artemesia glauca Pall.
Brauneria augustifolia (D. C.) Heller
Liatris punctata Hook.
Potentilla arguta Pursh.
Rosa pratincola L.
Anemone patens var. *Wolfgangiana* (Bess.) Koch.
Amorpha canescens Pursh.
Glycyrrhiza lepidota (Nutt.) Pursh.
Peralostemum purpureum (Vent.) Rydb.
Symphoricarpos occidentalis Hook.

The cactus, (*Mammilaria vivipara* (Nutt.) Haw.), is common over much of the dry sandy soil and prickly pear, (*Opuntia fragilis* (Nutt.) Haw.), has been found in several areas. *Bouteloua gracilis* is perhaps the most common grass and one of the more important for grazing. Wolfberry, (*Symphoricarpos occidentalis* Hook.), is a widespread shrub forming patches up to several acres in extent.

(3). ALKALI LAKES. About the "alkali" lakes and the more or less

dried flats of previous lake beds are found plants of species of the genera *Juncus, Scirpus, Carex, Chenopodium, Triglochin, Atriplex* and *Salicornia.* Away from the margins of the lakes or flats these plants intermingle with the prairie plants without forming any distinct boundaries.

(4). SANDHILLS. The flora of the sandhills is not strikingly different from the prairie surrounding them. The grasses and herbaceous plants are identical. The flora differs, however, in that many of the slopes of the hills, generally the north or east, are clothed with dense stands of the chokecherry, (*Prunus virginianum* L.) the wild plum (*Prunus americana* Marsh.), the Juneberry (*Amelanchier alnifolia* Nutt.), and the quaking aspen (*Populus tremuloides* Michx.). The bur oak (*Quercus macrocarpa* L.) and the box elder (*Acer negundo* L.) are commonly interspersed with other trees or shrubs. *Salix* spp. occur in clumps in the damper depressions.

V. INFLUENCE OF THE CLIMATE

A. TEMPERATURES

Temperatures, of course, exert a conspicuous and primary influence upon the activities of these ants. Their influence may be divided into: seasonal and daily.

1. SEASONAL INFLUENCE

The cold of winter necessitates hibernation and the complete cessation of all activities. Early spring is likewise too cold for activity but in normal years, early in April, the warmth of the heightening sun causes the ants to emerge. Freezing temperatures at night do no harm; the ants may be out on the nest moving sluggishly about during the day at a temperature close to freezing.

Later in the spring they are really active and commence to build up their nest and gather food industriously. Summer is the time of greatest activity, although hot weather curtails activity during the middle of the day. They maintain considerable activity in gathering food all during the fall and normally are active until well on in November. The second week in November 1931 they were slightly active during the day at temperatures from 44°F. to 57°F. (7°C. to 14°C.), though the temperatures at night ranged from 22°F. to 29°F. (—6°C. to —2°C.).

2. DAILY INFLUENCE

Temperatures at night, except in the summer, are too low for activity. During the summer numbers of workers are found on the nest and even wandering about the surrounding vegetation until well into the night. The coolness of the period before dawn causes them to retire and they do not again come out until the sun's rays strike the nest.

Except during early spring and late fall the morning is the time of greatest

activity. In the early morning the ants use the sunlit nest-openings; later as the temperature rises and the sun strikes directly, they avoid the openings in the sunlight and use only those which are partially or wholly shaded by the surrounding vegetation.

In the spring and fall the middle of the day is a time of considerable activity, but during the summer little is then accomplished above the nest. When the temperature is in the eighties Fahrenheit (= around 30°C.) or higher and the sun beats directly down upon the nest without the alleviating effect of a cooling breeze there is practically no activity. A few openings of the nest may be partially shaded during these hours and only from these do ants emerge. Partly because of the desiccating effect of the sun's rays paths are constructed under and through the vegetation to the plants upon which the aphids are pastured and to hunting territory. These semi-covered runways may extend up the sides of the nest to one or two major openings. A few workers occasionally emerge to run quickly about on the mound and then go back down, as if scouting hurriedly. When a passing cloud temporarily obscures the sun, numbers of workers quickly come out and scatter about the periphery, only to return when the sun shines again. Single workers, however, have been observed on the nest even at a temperature of 103°F. (39.4°C.).

Although in the evenings during the spring and fall there is little or no activity, during the summer their evening activity is second only to that of the morning. Even after dusk they continue building and repairing the nest and foraging about for food, the temperatures remaining in the sixties or seventies Fahrenheit (15°C. to 25°C.) until several hours later.

In summary, then, the ants are most active at temperatures in the sun between 50°F. (10°C.) and 80°F. (27°C.) or in the shade between 60°F. (15°C.) and 90°F. (32°C.), provided the relative humidity is above 25%.

B. LIGHT

In North Dakota *F. obscuripes* has a decided preference for nesting in open situations. Nests are rarely found in woods, never in dense woods, and all nests are exposed to sunlight for a large share of the time.

Full sunlight during the entire day does not curb their activities unless accompanied by high temperatures and low relative humidities. On the contrary it is conducive to their maximum activity. When the winged ants are emerging they wait for sunny periods to take flight, other meteorological conditions being favorable.

On evenings of hot days during the summer the workers are very active in food-gathering and nest-building until dusk. At these times the period from shortly before sundown to dusk is the time of activities second only to the early morning hours.

Long after dark in the summer workers are found slowly crawling about

the nest as if on patrol. Probably little is accomplished after dusk, however, as much of their prey is not moving about.

C. Winds

North Dakota lies in a region having considerable windy weather, which at times exerts an appreciable effect upon the activities of the ants.

The harmful effects of the wind are evidenced by the loosening of the thatch and even the blowing away of some of the twigs where the nest is exposed. Ants are forced to suspend their activities above ground if a strong wind, particularly when laden with dust or sand, sweeps across the nest. As noted later, winds prevent emerging of the sexual forms for the marriage flight.

D. Humidity

During the summer of 1930 I made a number of relative humidity measurements in connection with the activities of *F. obscuripes* with the following results:

The sexual forms emerged only at temperatures above ca. 60°F. (15°C.) when associated with a relative humidity above ca. 50%.

A few workers were active in shaded spots even when the relative humidity was as low as 17% at temperatures in the nineties Fahrenheit (thirties Centigrade) but were not active in the sun at relative humidities of 40% to 50% even when the temperature was 10°F. to 20°F. (5°C. to 10°C.) lower. There were no ants above the nest surface at a relative humidity of 14% when coupled with temperatures above 90°F. (32°C.).

During light rains the ants continued their activity.

In general, one might say the ants are active at relative humidities above 25% and may continue their activity at relative humidities even lower, provided they can avoid direct sunlight. The combination of the sun's rays and low humidities probably has a desiccating effect upon them.

E. Rainfall

Formica obscuripes adapts itself to considerable variations in rainfall as shown by the thriving colonies in the semi-arid western part of the state and those in the more humid Red River "Valley". That it endures the wide range in annual rainfall from 5 to 35 inches (13 to 89 cm.) shows a considerable degree of adaptability.

Drouths of a month or more during the summer do not retard activities, except when low humidity prevents the ants from being active above ground and in the sunlight during the middle of the day.

During a moderate rain the ants continue their normal activities and seem not at all hindered. Since the aphids from which they receive considerable nourishment are frequently stationed on the under surface of curled leaves, "milking" may be continued even during a rain.

F. PRAIRIE FIRES

Prairie fires are a factor of some importance in areas of the state where there is considerable grassland.

In McHenry County prairie fires are not infrequent and are detrimental in two ways: first, they set fire to the twig mound and may burn it out, resulting in a serious set-back to the colony, particularly when the brood is in that part of the nest; second, by burning the vegetation, prairie fires destroy the food of the insects forming a large part of the prey of the ants; these insects are driven out when not actually killed. The fires kill not only the vegetation upon which the aphids feed but also the aphids themselves, thus destroying the other main source of food.

VI. RELATIONS OF PLANTS AND *F. OBSCURIPES*

A. INIMICAL RELATIONS

The encroachment of grasses, herbs, and shrubs constitute an ever present menace to the mound. Particularly is this true in wet seasons when vegetation is growing luxuriantly. At such times plants grow up through the nest, and the efforts of the ants are not very effective. I have seen them actually gnaw grass blades down or cut them in sections, but it is doubtful whether they could cut down large vigorous weeds, herbs, or shrubs. Later in the summer, when the nest interior is dry, the plants probably die out from lack of moisture rather than from the activities of the ants.

In the nests are sometimes found roots of shrubs which may have been killed by the ants in building up their mound. Such roots are frequently removed to form tunnels which are used by the ants to connect chambers. In one case, stout plants of the grass, *Calmovilfa longifolia* (Hook) Scribn., had kept pace with the growth of the mound for some time, as shown by their bases being from 6 to 12 inches (15-30 cm.) below the crown of the nest; while they eventually were killed off from the summit of the mound, they maintained a very heavy growth on the periphery. The overshading of plants, even when not a result of actual encroachment constitutes a second menace. Colonies are driven out of nests when such plants as wolfberry become too dense about them and shade completely.

B. FAVORABLE RELATIONS

Plants are of benefit to *obscuripes* colonies in three chief ways:

(1). By affording food for aphids plants are of considerable importance. The proximity of wolfberry (*Symphoricarpos occidentalis* Hook.) growths and *obscuripes* nests is not fortuitous—wolfberry is attacked by aphids which in turn afford an important source of food to the ants. Wild liquorice, *Glycyrrhiza lepidota* (Nutt.) Pursh., is similarly the host plant of the same aphid which in turn is tended by *obscuripes*. Other plants include *Populus*

tremuloides Michx., *P. deltoides* Marsh, *Salix* spp., *Artemesia cana* Pursh., *A. glauca* Pall., *A. longifolia* Nutt. and *A. tridentata* Nutt. and *Rosa pratincola* L.

(2). Plants furnish the material out of which the thatch nest is constructed. Small twigs from shrubs, grass blades, and herb stems are universally used, though in varying proportions.

(3). Plants, of course, are the ultimate source of food of *obscuripes.* The chief source of food of this ant is insects, which either feed directly (membracids, grasshoppers, and aphids) or indirectly on plants.

VII. OTHER INFLUENCES

Besides the more important influences of the climate and vegetation there are other influences at work upon the distribution or activities of *obscuripes* colonies:

(1). Physiographic Influences. As a whole, the physiography of the state is favorable to the establishment of *obscuripes* colonies. There are, however, limited areas unfavorable to them. Such areas are the steep, bare slopes of hills and buttes, chiefly in the Missouri Plateau; the damp margins of sloughs, marshes, and lakes of the rest of the state; and areas along streams subject to seasonal overflow, or at the base of buttes subject to the run-off from their bare sides.

(2). Man exercises an appreciable effect upon *obscuripes.* By cultivation of large areas of the state, he prevents the establishment of mounds in the fields and drives them to the margins. At the same time, the cultivation of crops attracts hordes of insects, particularly grasshoppers, the chief prey of the ants. The destruction of woodlands increases the nesting area, while the establishment of groves lessens the area. By bringing in herds of domestic animals he adds a new danger to the nest, i.e., trampling; but probably not of more consequence than in the days of the vast herds of bison.

(3). The influence of other animals is sometimes appreciable. The kingbird, *Tyrannus tyrannus* (L.), has frequently been observed capturing the winged *obscuripes* as they fly away from the nest. In fact one kingbird stationed itself upon a tree a short distance from an *obscuripes* nest and with great regularity captured the winged ants as they flew by, one after another. The Arkansas kingbird, *Tyrannus verticalis* Say., has also been observed near nests, feeding upon insects, presumably including the winged *obscuripes.* The flicker, *Colaptes auratus borealis* Ridgw., is a well-known ant eater. It has frequently been seen on the ground near *obscuripes* nests and is very likely responsible for holes sometimes made in the mound. Bird feces composed entirely of *obscuripes* remains were found by a nest. The common crow (*Corvus brachyrhynchos* Brehm) has been observed eating the workers.

Newly captured toads, *Bufo hemiophrys* Cope and *B. woodhousei* Girard, readily ate many workers.

Lastly, domestic animals, particularly cattle, sometimes damage mounds by tramping upon them.

VIII. THE NEST

A. Form

The form of *obscuripes* nests varies considerably from a low, almost flat, crown to a paraboloidal structure. The occasional hollowed out surface of the nest, forming a "massive rampart", described by Muckermann (1902) for *obscuripes* nests in Wisconsin has not been seen by me.

The nest is invariably a superstructure of twigs, herb stems, or grass stems constructed above the chambers in the soil. These nest materials will hereafter be referred to as thatch.

On the open sandy prairie this superstructure of thatch is frequently built upon a slight eminence of soil, which is doubtless the result of excavating the soil chambers. Among shrubs or in less sandy soil, however, the thatch superstructure rests directly on the ground.

The form of what may be termed secondary nests is similar to that of the main or primary nest except that the roots of plants furnish the nucleus about which thatch is placed and tunnels excavated. Such secondary nests are generally connected by a well-defined runway to the main nest. These roots of plants were originally preyed upon by aphids which were tended by the *obscuripes* workers. As the ants excavated the soil about the roots an arborescent chamber developed which upon the death of the plant or even while still alive, was easily made into a small secondary nest. A secondary nest may eventually develop into the chief nest of the colony.

The form of the thatched crown is always in a state of change due to the activities of the ants and to the action of the environment. The changes are brought about by:

(a). Work of the ants themselves. If there is one thing that impresses the observer of a colony it is the continuous building and repairing of the nest. Whenever any workers are above the nest surface, most of them will be engaged in altering, repairing, or adding to the thatch. They are continually changing the openings of the nest, both in number and position.

(b). Depressing action of rains and snow. The effect of rains and melting snows naturally is to level the thatch and make it more compact. While such actions are partly beneficial in that they render the nest more resistant to the elements, they are as a whole, harmful because the nest is made more susceptible to plant invasions and also is lowered with consequent shading by the surrounding plants.

(c). Destructive effect of severe winds. As mentioned before, wind-

storms are apt to loosen and even blow away portions of the thatch. Many nests, however, are protected by nearby vegetation.

(d). Destructive effects of other animals. Domestic animals, particularly cattle, sometimes trample upon the nests when grazing and damage them. Such damage, however, generally is repaired in a few days in favorable weather. Nests have frequently been observed with their openings excavated to a depth of several inches. From the circumstance that flickers (*Colaptes auratus borealis* Ridgw.) are frequently found in their vicinity and have been seen on the ground nearby and are known ant eaters it seems highly probable the openings were made by them in searching for ants.

The peculiar behavior of two pet crows indicated an unexpected factor which may, perhaps, be of some importance. These crows, entirely normal in every respect and able to fly as well as any wild ones, several times flew to the nest while I was observing the general activity. They stood upon it, fluffed out their feathers, squatted in the manner of birds taking a dust bath, and deliberately allowed the ants to crawl over them. The workers swarmed in large numbers over and through their fluffed out feathers, spraying formic acid liberally. After a few moments, when covered with ants, they hopped off the mound and shook themselves vigorously. Those ants that were still clinging to the feathers were picked off and thrown aside; none was eaten. It seemed to me the crows might have acted in this manner to disinfect themselves: the formic acid sprayed by the ants might repel the ectoparasites of the crows. The effect of this behavior to the nest was to scatter the thatch and flatten the nest appreciably.

B. SIZE

1. MOUND PROPER

The size of the mounds of *obscuripes* is highly variable. The height of the mound varies from an inch (2.5 cm.) or less in young nests to a maximum of 18 inches (45.7 cm.) in populous, flourishing colonies. The average height is about 8 inches (20 cm.) for typical nests. The diameter of the entire mound, including the soil base (when present) varies from a maximum of 11 feet 3 inches (343 cm.) to about one foot (30.5 cm.). The average typical nest is from two to three and one-half feet (60-110 cm.) in diameter. The diameter of the thatch part of the nest, alone, varies from a maximum of eleven feet (335 cm.) to a minimum of 5 inches (13 cm.), averaging about 17 inches (43 cm.). The disc area of the entire nest varies from about 98 square feet (9 sq. m.) to 0.8 square feet (0.07 sq. m.).

The thatching material extends down below the surrounding soil level to a depth of about 10 inches (25 cm.) or about 18 inches (45.7 cm.) below the top of the mound. The topmost soil chambers are made very large and close together and are filled in with thatch. The quantity of thatching material, mostly twigs, from an average nest was 0.75 bushel or 25.6 liters.

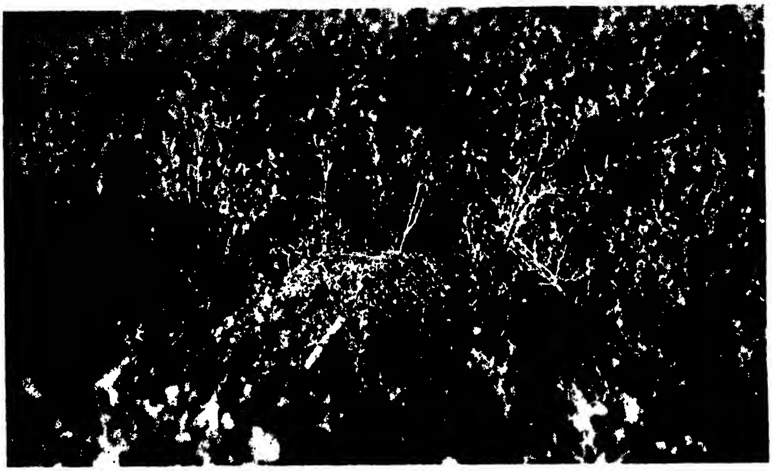

FIG. 2. Typical twig nest in *Symphoricarpos occidentalis* patch. Six inch (15 cm.) ruler at base.

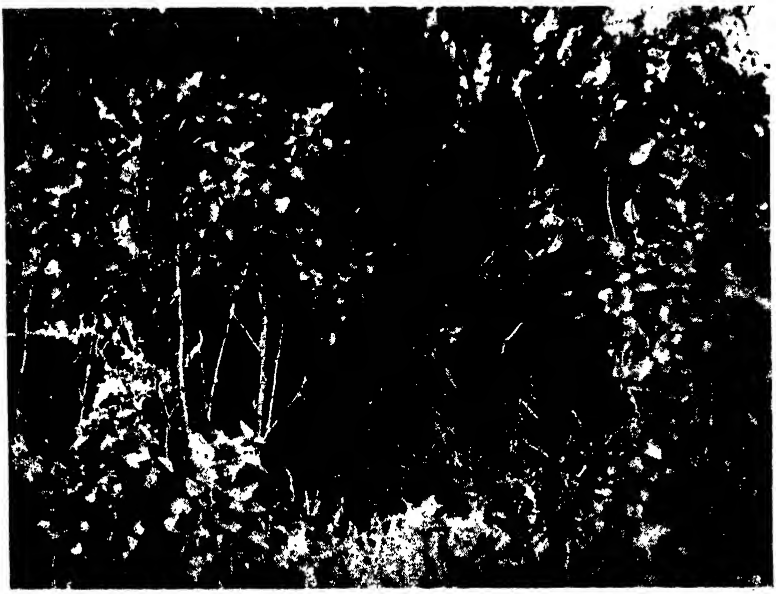

FIG. 3. Nest in margin of bushes.

The thatching material has a composition varying according to the immediate plant environment. Nests in or near wolfberry (*Symphoricarpos occidentalis* Hook.) patches are of coarse wolfberry twigs mixed some finer material of grass and herb stems. Nests on the prairie at some distance from shrubs consist of somewhat finer material from grasses and herbs. Occasionally a nest is found thatched with fine grass stems which form a more compact

mound. Such nests are low and quite flat and seem to be inhabited by young colonies of small populations.

The typical *obscuripes* mounds are of coarse twigs from a fraction of an inch (1 cm.) to as much as eight inches (12 cm.) in length and usually about 1/16 inch (1-2 mm.) in diameter.

2. CHAMBERS IN SOIL

The lower part of an *obscuripes* nest, i.e., the chambers in the soil beneath the mound proper, furnishes a suitable place for the young brood and a safe place for hibernation.

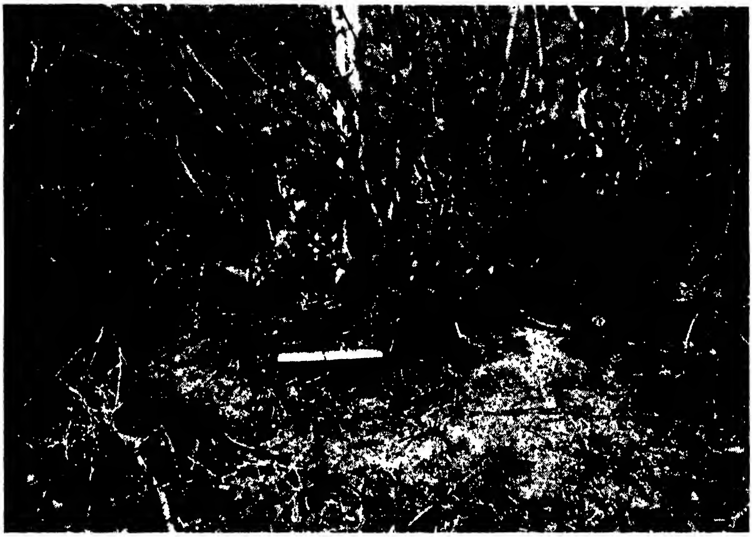

FIG. 4. Young nest, showing soil periphery, at base of bushes. 6 inch (15 cm.) ruler on nest.

Chambers in the soil extend laterally less than the diameter of the entire nest but may be of greater or lesser expanse than the diameter of the thatch. Tunnels and chambers are excavated in the soil to a maximum depth of 62 inches (157.5 cm.). The minimum depth for the lowest chambers was 53 inches (135 cm.). The average depth was 57 inches (145 cm.), indicating a remarkable uniformity.

Hardness of the soil does not seem to be a serious limiting factor. In McHenry County the soil is not rocky and bed-rock is hundreds of feet below the surface. Generally the soil is sandy to a depth of several feet at least and below this it is a mixture of clay and sand. This clay-sand mixture is frequently very hard packed but penetrable by the ants.

The important limiting factor is the water table. In McHenry County it lies at a depth of 6 to 8 feet (180-245 cm.). Below about 5 feet (152 cm.), the soil is so damp that when squeezed the expressed water wets the hand.

This is apparently too wet for the ants and their chambers are never found at this depth.

C. AREA PATROLLED BY COLONY

The territory patrolled by the workers of a single colony is difficult to determine. The area can be indicated, however, by the paths which these ants make radiating out from the nest. These paths are clearly made near the nest and follow the ground closely, going beneath leaves, fallen stems, and other material so that in reality they are partially covered runways. The workers traverse these regularly in going to and from the aphids, and in bringing in prey.

On September 8, 1931, such a path was watched for two minutes from 7:36 to 7:38 A.M. at a point three to four feet (0.9-1.2 m.) from a nest. The path led to a wolfberry patch on the partially dried leaves of which still remained a few aphids. In those two minutes 11 workers passed towards the nest and 6 in the opposite direction. They were mostly minima workers and all traveled quite leisurely, keeping close to the path. A few minutes later, on the same morning, a path about 3 feet (0.9 m.) from another nest which was 90 feet (27 m.) away from the first nest was watched. In one minute 22 workers passed going towards the nest and 12 away, towards the wolfberry patch.

The maximum length to which an ant path was traced was 70 feet (21.5 m.). I have, however, found a worker 156 feet (47.6 m.) from the nearest nest. A worker was once noticed dragging a noctuid larva towards its nest, 13 feet (4 m.) away over a path which extended farther into the wolfberry patch. Paths were frequently traced three to ten feet (0.9-3 m.) from nests before being lost.

Ant paths generally lead toward areas where there is an abundance of plants upon which aphids are pastured. These paths are best developed toward wolfberry and *Artemesia glauca* patches or to the bases of *Rosa pratincola* bushes.

The extent of territory of a colony can only be very roughly estimated from such data, but it seems probable that the workers from an average colony have a territory at least of 1,000 square feet (35 sq. m.) and probably much more.

D. THE BROOD CHAMBER

In April the first brood consisting of eggs is found in soil chambers at a depth of one to two feet (30-60 cm.). Later in the spring, eggs, larvae, and pupae are found at about the same depth. It is only during the summer that the large conspicuous brood chamber is developed. This chamber, which is very incompletely divided by twigs running through it at all angles, is

generally at the base of the thatch part, resting upon the highest soil chambers. It is about 6 inches (15 cm.) high and is enclosed by thatch from 3 to 10 inches (7.6-25.4 cm.) thick. In some cases the floor is also of thatch but in others of soil. The chamber is roughly ellipsoidal in shape; one chamber measured 4 x 3 x 3 inches (10 x 7.6 x 7.6 cm.) and another 10 x 8 x 6 inches (25 x 20 x 15 cm.).

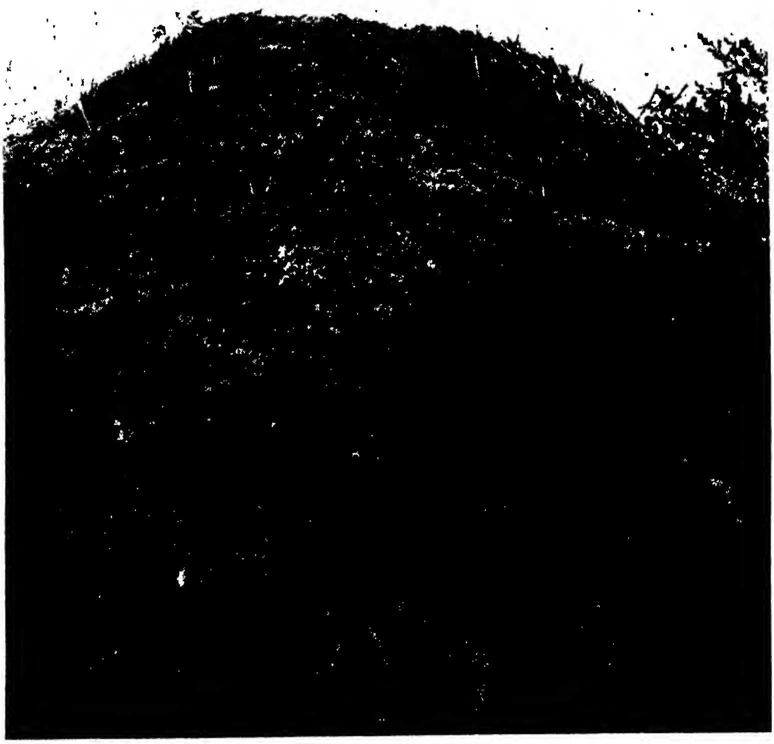

FIG. 5. Section of nest on the prairie showing central brood chamber (filled with thatch) and soil chambers beneath. Thatch superstructure is unusually compact and soil filled as a result of the severe duststorms of the spring of 1934.

Pupae and callows are kept in the upper part of the chamber while eggs and larvae are to be found in the basal part and in the uppermost soil chambers.

In the fall, after the brood has all emerged, the brood chamber is filled with thatch; hence no brood chamber is present from fall to spring.

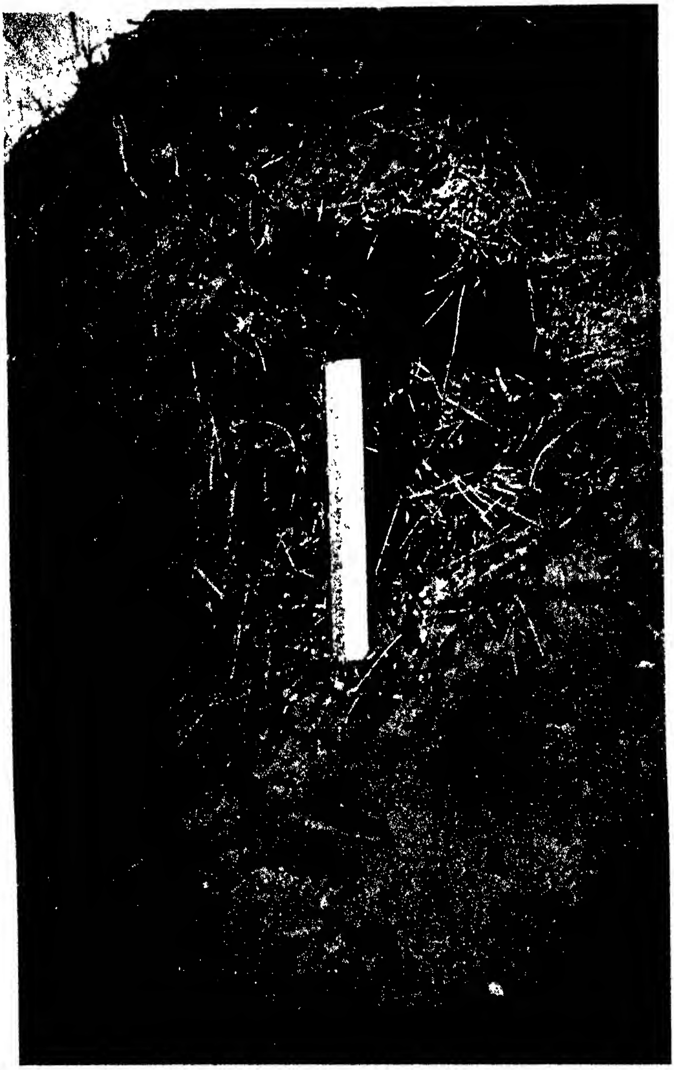

FIG. 6. Section of nest on the prairie showing location of the brood chamber by the 6 inch (15 cm.) ruler. Thatch superstructure has an unusual amount of soil as a result of the severe duststorms of the spring of 1934.

No clear evidence was found showing that the presence of the workers or the brood raised the nest temperature. The brood chamber is so situated as to be effectively insulated and doubtless retains for some time heat absorbed during the day. During rainy periods the chamber is well drained and can dry out quickly. These are probably optimum conditions for rearing the brood.

E. TEMPERATURES

Andrews (1927) found in the case of *Formica exsectoides* F. that inside temperatures of the nest were higher than the surrounding earth and were due to heat received from the sun.

In the case of *F. obscuripes* inside temperatures of the thatch were also found to be higher than the surrounding earth and were likely due to the heat-absorbing and heat-retaining qualities of the thatch. The presence of the brood or workers probaby had no effect upon the temperatures.

Below the thatch part there is a regular drop in temperature from the highest to the deepest chambers. The temperatures of the lower soil chambers are nearly constant all summer but show a gradual increase as the summer progresses.

F. NUMBERS OF NESTS

Formica obscuripes colonies may be absent over large areas of the state which are seemingly well suited to them and abundant in other limited areas. They do not, however, appear to be associated in such large numbers as are those of *Formica exsectoides*. It is not uncommon to find several nests a few rods (10-20 m.) apart, but additional nests are likely to be much farther away. The greatest numbers of *obscuripes* colonies found were in the sandy park-like country containing numerous, more or less continuous *Populus tremuloides* groves north of Towner. In a distance of 150 feet (45.8 m.) along the west side of such a grove were found twelve small nests. Numerous *Formica fusca* colonies were significantly present. An abundant source of food was the secretions of aphids found in great numbers on the *Populus* trees.

IX. NESTING SITES

Formica obscuripes in North Dakota is conspicuously an ant of the open and not of woodlands. The nests have always a long exposure to sunlight, many being exposed to the very maximum amount of light possible. The nesting sites chosen by *obscuripes* may be classified on the basis of the exposure, viz., those having full exposure and those having partial exposure.

A. FULL EXPOSURE

Nests having full exposure, *i.e.,* those not shaded to any appreciable extent during the entire day, are common throughout the state. Such nests are built among grasses and herbs at some distance from trees. They may be located in a great variety of places—on level or rolling prairie, in valleys, on sides and crests of hills, along roadsides, and in pastures. Dr. G. C. Wheeler has found nests upon the summits of Sentinel Butte and Black Butte (the two highest points in the state) and only a few feet from the precipitous sides.

B. Partial Exposure

While most *obscuripes* nests are built in places affording a full exposure, there are limited areas throughout the state where mounds are established in places shaded to a greater or less degree.

As mentioned before, the wolfberry, *Symphoricarpos occidentalis,* is a widespread shrub of the state, occurring in patches up to several acres in area. It is attacked by the aphid, *Aphis symphoricarpi,* and perhaps others. This aphid is frequently found tended by *Formica obscuripes* and this association of wolfberry, aphids, and *obscuripes* nests is common. Such nests are usually built in the margins of the patch and may be somewhat shaded by the shrub on one or more sides but never completely shaded.

Dense growths of grasses about the nest sometimes results in partial shading, usually of only one side. However, several nests of *obscuripes* were found completely hidden by the grass, *Calamovilfa longifolia.* The grass grew to a height of four feet (122 cm.) and completely hid the nest. In these cases the grass was probably choking out the colony.

A third condition of partial exposure is afforded by those mounds in grassy glades in groves of the quaking aspen, *Populus tremuloides,* near Towner. This association approaches the association of *Formica rufa* in the forests of Europe. Occasionally nests are shaded to some extent for a large part of the day. They are not built in locations too shady to permit a growth of grasses.

A case of partial exposure, hardly typical, was a mound found by Dr. G. C. Wheeler on the summit of Black Butte partly overgrown with the creeping juniper, *Juniperus horizontalis* Moench. Only a few ants were found in the mound and the colony was probably being crowded out by the juniper.

The sagebrush flats of the Little Missouri River and its tributaries afford a condition of partial exposure similar to that of the wolfberry. Nests are sometimes established close to the sagebrush and are protected and shaded by it on one or more sides. It is unlikely that they are ever completely shaded by the shrubs.

In the Turtle River Valley are found nests in comparatively shady situations. Here on the grassy valley floor *obscuripes* nests on the very margins of open deciduous woodlands. The shading is never dense but the trees afford some shade and considerable protection. A striking exception, however, was an enormous nest found north of Arvilla which was completely surrounded by trees. The nest received very little direct sunlight. It was distinctly not typical in shape and size as well as in location.

X. LIFE HISTORY

A. COLONY FORMATION

It has not been my good fortune to actually observe the founding of a colony of *Formica obscuripes*. However, that harbinger of colony formation, the marriage flight, has been observed in two successive summers.

Mating among ants is generally accomplished on the marriage flight or swarming of the winged sexual forms. But judging from my own observations *obscuripes* seems to have no true marriage flight. The winged sexual forms merely emerge from the nest singly or a few at a time and take flight. Fertilization by this method seems very hazardous. Local popular accounts of the swarms of winged ants always refer to much smaller ants. I have never found an observer of swarming winged ants as large as *obscuripes*.

Dr. W. M. Wheeler suggests that this situation may parallel that in middle Asia described by Kuznetzov-Ugamsky (1927). The latter states that only those ants which can modify their marriage flight to meet the harsh conditions prevailing in this steppe and desert regions are able to flourish and extend their range. The genus *Cataglyphis*, for example, has a modification of the marriage flight in which the winged sexes run about the surface of the ground and take long leaps (*Sprünge*). There is no true nuptial flight.

It may be that *F. obscuripes* in North Dakota has modified the typical marriage flight, even more than the parent stock *F. rufa*, to fertilization in the nest, or, at the most, on the ground, because of the windiness of the region at this time of year. The genus *Myrmica* forms a typical marriage flight in the same region but it takes place in late August and early September. United States government weather records show that wind movement is less in September than in June and least in August of any month of the year.

The winged males and females wait for favorable weather conditions before taking flight. When the air is calm, the sky quite clear, the temperature above 60°F. (15°C.), and the humidity above 50%, the ants take flight. In so doing they climb up a grass blade or herb stem, vibrate their wings for a moment as if to try them out, then fly upwards and are generally carried by a slight breeze until out of sight, which is a matter of 40 feet (12 m.) or more. Commonly but one or a few take flight at the same time but, whether of the same or the opposite sex, they do not fly in a group. Thus there is not the least indication of a nuptial flight. As a rule but one sex is present upon the nest at any one time, though when both sexes are present there is no interest displayed between one another. Winged ants may emerge from several nests in the same vicinity at the same time but have never been seen to fly off together. They begin to emerge early in June and may leave the nest irregularly for a month. Many of these winged ants were collected with one or

more wings crumpled or even dwarfed so that they could not fly, although they attempted to take flight in the same manner as the normal winged.

In all probability *obscuripes* follows the other Formicas of the *rufa* group in founding colonies outlined by Wheeler (1933, p. 156) by "temporary, or protelian, social parasitism". By the conciliatory type of this method the "female invades nest of the host species and is adopted by the workers after acquiring the brood and nest-odor. Host queen probably killed by her own workers". The workers "rear the successive broods of the parasite. Eventually the host species dies out and a pure colony of the parasite survives."

That this is the method likely used is supported by the coincident range of the *Formica fusca* group, the host species. Furthermore, the greatest numbers of *obscuripes* nests found by me were interspersed with numerous *Formica fusca* crateriform nests.

Muckermann (1902, p. 356) states that in Wisconsin a new colony of *F. obscuripes* is formed thus: a "little squadron sallying forth to establish a new foundation no sooner discover a warm, sunny place, than they begin to dig a few holes in the soil, when there arises gradually a little hill." He does not say whether one or more queens are brought along but I assume such must be the case. I have never seen such a "little squadron" so occupied.

B. The Brood

The brood of *Formica obscuripes* in North Dakota is probably not carried over the winter but raised to maturity between spring and autumn.

The time required for development, when kept in the laboratory at room temperature of about 63°F. and 72°F. (17°C.-22°C.), varies from 61 to 122 days. These periods agree singularly well with developmental periods found by Miss Fielde for *Aphaenogaster fulva* and by Janet for *Myrmica rubra,* as reported by Wheeler (1910, p. 81), of from 54 to 141 days and 71 to 117 days respectively.

The milky white egg is ellipsoidal, with a length of about 0.60 mm. and diameter of about 0.31 mm. Eggs have been found in nests as early as April 30, and as late as August 14. Those kept in the laboratory at a room temperature from 63°F. to 72°F. (17°C.-22°C.) developed into larvae in a minimum of 23 days and a maximum of 53 days.

Youngest larvae are of about the same length as the egg and develop to a maximum size of about 6 mm. in straight-line length. Larvae have been found in nests from June 6 to August 22. Kept in the laboratory at room temperature of about 72°F. (22°C.) they developed into the pupal stage in a minimum of 7 days. At 63°F. to 68°F. (17°C.-20°C.) they pupated after 7 to 33 days.

Male and female pupae are about 9 mm. in length, while the worker pupae vary from 3.5 mm. to 7 mm. Sexual pupae have not been found in nests later than June 20, but worker pupae have been found from June 11 to

September 9. The length of the worker pupal stage when kept in the laboratory at a room temperature of from 63°F. to 68°F. (17°C.-20°C.) was from 31 to 93 days.

The callow stage lasts only one or two days. The sexual forms and some workers scarcely have a callow stage but emerge directly from the cocoons into adults and are able to move about normally in a few hours.

C. Division of Labor

Each worker caste has fairly well-defined duties among the various activities of a colony.

Most of the activities of the minima workers are concerned with foraging and the care of the brood. Both minima and media, but chiefly the minima, workers are occasionally seen bringing up a larva or pupa from a nest opening, carrying it about for a moment, and then taking it back. While this behavior is frequently exhibited after a rain, the young do not seem abnormally moist but appear normal in every respect. The minima workers also are many times observed carrying out empty cocoons from the nest to the periphery. In short, the minima workers act as the chief nursemaids.

Workers found on the ant paths are chiefly the minima and media. They are the ones observed dragging prey to the nest and tending aphids. Very rarely is a large worker observed near an aphid colony.

While all sizes of workers take part in the building and repair of the nest, the maxima are especially active. They are, moreover, the most aggrsssive and effective in the defense of the colony, although all sizes are pugnacious and rush to its defense.

XI. POPULATION

The census of a representative *obscuripes* nest was taken in late August and early September, 1931. A rather large nest was selected which was 16 inches (40.6 cm.) high and 54 inches (137 cm.) in total diameter. The nest was surrounded and completely hidden by a dense growth of the grass, *Calmovilfa longifolia* (Hook.) Scribn., but seemed flourishing. There was another *obscuripes* nest 300 feet (91.4 m.) away, but there was no evidence of any communication between the two.

The first method used was to allow the workers to crawl upon my hand placed upon the nest, and then to brush them off into a small pail with a layer of carbon bisulphide in the bottom. While with this method many were secured at the beginning of the afternoon's collecting, the numbers of those rushing out to grasp my hand soon dwindled, and another method was then used.

Handfuls of the nest were taken up and placed in the middle of a large piece of canvas. As the ants crawled to the periphery they were picked off. This was the method generally used.

A third method was to pick up the ants individually from the nest or the cavity as I dug down.

Using these tedious methods with the assistance of several helpers, in the course of eight afternoons and a total of sixteen hours of labor most of the inhabitants were collected.

The ants, all workers, were then counted individually and a total of 16,481 was thus secured. Many cocoons and callows were dug up but were not counted since the adult population was desired. These, which would probably become adult workers in a few weeks (before the onset of winter) would probably add at least two thousand to the total inhabitants. The workers which escaped the census may have numbered 500, probably not much more. The total population of this large sized nest may thus be considered to be about 19,000.

Yung (according to Wheeler, 1913) has found for the larger nests of *Formica rufa* in Europe a population of from 20,000 to 94,000. He found, furthermore, that population of the colony did not vary with the size of the nest; the largest nest counted having scarcely half the population of the next to the smallest mound.

Until further counts of *obscuripes* are taken it may be assumed that the population of the nests will not exceed 40,000. Although in the typical *rufa* there appears to be no direct correlation between the population and the size of the nest, in the case of *obscuripes* there may be a direct relationship. Small nests have been watched and the numbers of workers about the nest are considerably smaller than those of large nests. I suspect that the size of nests of *obscuripes* indicates the size of the colony, because only a populous, flourishing colony can maintain a large twig nest. Were a small colony to occupy a large nest the numbers of workers would probably be too small to maintain the mound against the depressing effect of water and the destructive effect of winds.

XII. DAILY AND SEASONAL ACTIVITY

The daily activity of the workers varies directly with the seasons.

In the winter, since they are hibernating in the earthern chambers a few feet below the surface, there is no activity. A thaw during the winter may draw the workers in the higher soil chambers up into the twig part, but colder weather forces them down again; there is nothing they could do if they did come out.

The workers emerge early in April in average years. During the warm part of the day they come forth and slowly mill about, seemingly enjoying the warmth of the sun's rays. At first, their activity is confined to repairing the damage wrought by the snows and thaws of winter. Later, when the hordes of insects emerge, they take up the serious occupation of getting food.

At the same time they repair and build up the nest. The developing brood must be cared for and, when the weather gets warm enough, carried up into the rebuilt brood chamber.

The summer, particularly the early summer, is the time of their greatest activity. The brood requires more care, the emerging workers and sexual forms needing much attention. From early in the morning until late in the evening the workers forage about for food, taking a "siesta" only during the hottest, driest part of the day. Many are occupied in attending aphids.

During the fall they are especially active in gathering food until well on in October or November, or until all their prey is gone and the weather gets too cold. Nest building and repair takes most of the time. Only pupae are left to attend to in the early fall; after they emerge there is no brood to care for. The ants go into hibernation in November after continued cold weather or the arrival of snow.

XIII. FOOD

A. Methods Used to Obtain Data

During all hours of the day three nests at Towner were observed continuously for periods of an hour or less. At such times only a portion of the nest was in full view, because vegetation hid some of the openings on the sides. Hence, not all of the food brought to the nest at the time of observation would be seen. The food observed brought to the nest likely constituted a representative amount, however.

B. Methods Used by the Ants in Obtaining Food

The food, other than aphid secretions to be considered later, was dragged by one or more workers to the nest. In the great majority of cases the prey was already dead by the time it reached the nest. In many cases parts of insects were taken; sometimes several parts of what seemed to be the same insect were dragged successively to the nest. A specimen of *Coccinella 5-notata* Kby. was collected as it was being dragged down an opening of the nest, still alive and struggling. A *Ludius elegans* (Kby.) was also collected on a nest, still alive and struggling with a number of workers.

A possible method of capturing prey is suggested by an observation made near a nest: a worker, clinging to a grass stem, seemed deliberately to fall two or three inches (5 or 7 cm.) to a moth fluttering beneath. Although it failed to capture the moth, its behavior indicated a method which may be employed.

Upon one occasion near a nest three workers were observed investigating a membracid which was appressed to the stem of an evening primrose, *Oenothera pallida* Lindl. They climbed over and around it, touching it with their antennae; but the Membracid remained motionless, and the workers

shortly went away. If it had moved they probably would have tried to capture it.

The inedible parts of the insects used as food are either brought up and taken away from the nest, or stored in chambers within the nest. In several cases grasshopper, beetle, *Myrmica,* and *obscuripes* remains have been found stored in soil chambers between one and two feet (30-60 cm.) down the nest.

C. Natural Food

The natural food of *Formica obscuripes* was found to be derived mostly from two sources: insects and aphid secretions. Most of the insects listed below were taken from the workers as they were being brought to the nest. In many cases they were dismembered to a greater or lesser extent and sometimes seemed already partially eaten. A few spiders were also collected.

Not the slightest evidence was found to suggest that this ant might use plants as food.

1. Arthropoda

The following table, listing the arthropods used as food by *obscuripes,* includes only those specimens which I have collected directly from the workers or have found dead in the chambers of the nest. With the exceptions of the ants and spiders they were all identified at the United States National Museum.

ORTHOPTERA

Acrididae

Psoloessa delicatula? Scudd.................................adults and nymphs
Psoloessa? sp. ....nymph
Melanoplus bivittatus Say...adult
Melanoplus sp...5 small nymphs
Phoetaliotes nebrascensis Thomas...............................male nymph
Acridinae.......................................head and thorax of adult
Oedipodinae..small nymphs
Many grasshoppers, both adults and nymphs, which, because of their fragmentary conditions, could not be further determined.

Tettigoniidae

Orchelimum? sp.......................................very small nymph

COLEOPTERA

Scarabaeidae

Dichelonyx elongata Fabr...3 adults
Serica curvata Lec...5 adults

Coccinellidae

Coccinella 5-notata Kby.........................adults, including a live specimen
Hippodamia parenthesis Csy...adult

Elateridae

Ludius elegans (Kby.)...........................adults, including a live specimen

Chrysomelidae
Trirhabda sp. (*T. canadensis* Kirby?) .... adult
Carabidae
Harpalus sp. .... adult
Curculionidae
Anametis granulata Say .... adult
?*Hypera* .... headless pupa
Harpalidae
Harpalus herbivagus Say .... adult
Cantharidae
Podabrus? sp. .... adult

HEMIPTERA

Pentatomidae
Coenus delius Say .... adults
Peribalus abbreviatus Uhler .... adult
Neottiglossa undata Say .... adult
Coreidae
Alydus conspersus Montandon .... adult
Lygaeidae
Emblethis vicarius Horvath .... adult
Nabidae
Nabis subcoleoptratus Kirby .... 2 adults
Corixidae
Sp. of Corixidae .... 2 adults

HOMOPTERA

Membracidae
Ceresa bubalus (Fabr.) .... 4 adults, 3 nymphs
Ceresa sp. .... adult
Membracid .... adult

LEPIDOPTERA

Gelechiidae
Gelechia sp. .... larva
Olethreutidae
undet. larva ....
Noctuidae
Euxoa minis Grt. .... adult
Seven and possibly eight undeterminable species .... 10 larvae
Epizeuxis sp? .... larva
Feltia sp. .... adult
Tortricidae
Eucosma sp.? .... adult
Pyralidae
Pyraustinae .... larva
Crambus sp. .... adult
Thorax of moth ....

HYMENOPTERA

Braconidae
Bracon vulgaris (Cress.) .... adult
Hylaeidae
Colletes kincaidii Ckll.? .... adult
Andrenidae
Agapostemon angelicus Ckll. .... adult
Halictus (*Chloralictus*) *pruinosiformis* Crofd. .... adult
Sphecidae
Tachysphex tenuipunctus Fox .... adult
Formicidae
Myrmica scabrinodis sabuleti var. *americana* Weber (MS) .... workers and male
Lasius niger var. *neoniger* Emery .... females and worker
Lasius umbratus mixtus var. *aphidicola* Walsh .... workers

DIPTERA

Syrphidae
Sphaerophoria sp. .... adult
Asilidae
Asilus notatus Wied. .... adult
Chironomidae
Chironomus sp. .... adult
Limoniidae
Helobia hybrida Meigen .... adult
Bombyliidae
Anthrax moris L. .... adult
Sarcophagidae
Sarcophaga bullata Parker .... adult
Sarcophaga sp. .... adult
Wohlfahrtia meigenii Schiner .... adult

ARACHNIDA

Several spiders of the genera *Pellenes* and *Lycosa*.

It will be seen from the foregoing list that representatives of seven orders: Orthoptera, Homoptera, Hemiptera, Lepidoptera, Coleoptera, Hymenoptera, and Diptera include all the insect food collected.

In numbers of individuals, the Orthoptera formed the largest group, comprising about 26% of all insects taken. Most of the grasshoppers were brought to the nest in such a fragmentary condition that identification was difficult or impossible. One specimen was a tettigonid, all the rest were Acrididae. Of the latter, three genera, *Psoloessa, Phoetaliotes,* and *Melanoplus* were represented, each with at least one species. Specimens of *Melanoplus* were most numerous and include the species, *bivittatus* Say, one of the two most injurious grasshoppers of the state.

Lepidoptera formed the second largest group, comprising about 22% of all specimens. Of the five families represented, Noctuidae led with two-

thirds of all individuals. Most of the Lepidoptera were larval stages; they probably were the easiest prey of the ants.

Coleoptera constituted about 17% of all insects taken. Eight families and nine genera were represented, the genus *Serica* being the most numerous. Except for one pupa, all of the specimens were adults. Many larvae and pupae were found inhabiting the soil beneath the nest, and it is possible they are eaten if found.

About 12% of the insects were Hemiptera. Five families were represented, Pentatomidae predominating. All were adults.

Homopera also formed about 12% of the insect food. All of these were members of the family Membracidae. The destructive leaf hopper, *Ceresa bubalus*, in its nymph or adult stages constituted about three-fourths of all the specimens. No aphids were taken to the nest, either dead or alive.

Diptera constituted about 9% of the insect food. Six families were represented and all specimens were adult.

Hymenoptera formed the smallest portion, about 7%, of the insect food. Representatives of five families were present. All the specimens were adult. Only five cases of ants used as food were observed. A number of females of *Lasius niger* var. *neoniger* Emery were found in an *obscuripes* nest which had a colony of this species nesting in the margin. The position, apparently safe enough for the workers, was evidently dangerous to the sexual forms. Upon another occasion a dead worker *neoniger* was taken from *obscuripes* workers on their nest. The third case was the finding of two partially eaten workers of *Lasius umbratus mixtus* var. *aphidicola* Walsh in soil chambers of an *obscuripes* nest. Parts of *Myrmica scabrinodis sabuleti* var. *americana* Weber (MS) workers were found in refuse chambers. The ants were probably captured as they wandered near the *obscuripes* nest. The fifth record is of a dead male *americana* taken from *obscuripes* workers on their nest.

Several medium sized spiders formed the remainder of the natural food. Small spiders are frequent inhabitants of the nest and may be eaten when found.

2. CARRION

Carrion is sometimes eaten by these ants. Richardson ground squirrels, *Citellus richardsonii* (Sabine), have several times been shot and placed upon the nest. The ants would partially eat the carcass and then bury it within the nest, as they do any object too large or heavy to move away.

3. SECRETIONS OF APHIDS

The secretions of aphids constitute an important source of food and very likely are second in importance only to the bodies of insects. It is even probable that in some cases these secretions are the primary source of food.

Jones (1929, pp. 48-50) has listed nine genera with thirty-one species of aphids tended by *Formica rufa* var. *aggerans* Wheeler, *Formica rufa*

obscuripes Forel, and *Formica rufa obscuripes* var. *melanotica* Emery in Colorado. These three forms of *rufa* are here considered to be the same subspecies, *obscuripes*. The aphids were found upon twenty-one genera of plants. Two of these genera, *Populus* and *Artemesia*, include species which are similarly associated with *obscuripes* and aphids in North Dakota.

In McHenry County, where the habits of *obscuripes* were most studied, the identified aphids found tended by them were *Aphis symphoricarpi* Thos. and *Neothasmis populicola* (Thos.). One colony of *symphoricarpi*, however, had, according to P. W. Mason, "one specimen which seems to be *Aphis medicaginis* Koch". *Aphis symphoricarpi* was frequently found on *Symphoricarpos occidentalis* Hook and on *Glycyrrhiza lepidota* (Nutt.) Pursh. in the vicinity of *obscuripes* nests. *Neothasmia populicola* (Thos.) was found in large numbers with many males present in early June, 1932 on *Populus tremuloides*.

Mr. J. E. Goldsberry found *obscuripes* workers tending aphids on sagebrush (*Artemesia* sp.) in the southwestern part of the state, which were determined by the United States National Museum as apparently an undescribed species of *Bipersona*. Unidentified aphids, tended by *obscuripes* workers, were found in considerable numbers on the leaves of many plants of *Artemesia glauca* Pall. and, of a different species, on the petioles on young shoots of a willow tree (*Salix* sp.) in McHenry County. Unidentified aphids were also found on the roots of the widespread prairie rose, *Rosa pratincola* L. and on the young leaves and petioles of *Populus deltoides* Marsh.

The relations between the aphids and ants are apparently of mutual benefit. The ants are very pugnacious and rush to the defense of the aphids when molested. While of little avail against a large enemy they probably are valuable in driving away other insects which prey upon the aphids. Coccinellid beetles and syrphid flies, among the chief enemies of aphids (Jones, 1929, p. 10), were collected as food of the ants, which is an indirect way of protecting them.

D. Food in Captivity

Workers have been kept six months or more, queens nine and one-half months, and workers have been raised from the egg stage in observation nests. The food given them was, therefore, apparently satisfactory.

Various insects have been fed to the ants in captivity with successful results. Meal worms cut in pieces were the staple insects food. Grasshoppers, moths, house flies, June beetles, and various beetle larvae were readily eaten.

Honey and sugar were the other staple foods. Apparently the ants could live for months upon either. Other sweets, such as corn syrup, maple sugar, and sorghum, proved acceptable.

XIV. MYRMECOPHILES

The myrmecophiles which I have collected from *obscuripes* nests, identified at the United States National Museum, may be classified, following Wheeler (1910, p. 380), into:

(a). Persecuted Intruders, or Synechthrans. Under this heading probably come the scavenger staphylinid beetles:

Philonthus agilis Grav.
Philonthus debilis Grav.
Philonthus theveneti Horn
Goniusa obtusa Lec.
Atheta sp.
Aderocharis corticinus Grav.
Paederinae (*Gastrolobium* or related genus)
Platymedon laticollis Csy.

(b). Indifferently Tolerated Guests, or Synoeketes. Most of the myrmecophiles which I have collected probably are of this type:

COLLEMBOLA

Unidentified small white collembolans

COLEOPTERA

Scarabaeidae	Scarabaeid pupa
Scarabaeidae	*Euphoria inda* L. in pupal cells
Scarabaeidae	*Serica intermixta* Bltch. adult
Scarabaeidae	*Phyllophaga* sp. (*P. lanceolata?*, *P. corrosa Lec.?*)
Carabidae	*Amara* sp. adult female
Elateridae	*Melanotus* sp. larvae
Chrysomelidae	*Cryptocephalus* sp. larvae
Hydrophilidae	*Berosus* sp.
Cryptophagidae	*Atomaria* sp.
Histeridae	*Hetaerius?* adult

LEPIDOPTERA

Noctuidae	*Epizeuxis* sp.? larvae

DIPTERA

Milichiidae	*Phyllomyza securicornis* Fallen larvae
Leptidae	larvae
Anthomyiidae	larvae
Therevidae	larvae

ARACHNIDA

The spiders, identified by Mr. Nathan Banks, include adults and young of both sexes of the genera *Drassus* and *Erigone*. A specimen of *Xysticus ontariensis* Emert. and a male of *Thanatus lycosoides* Emert. were taken alive in nests.

Nearly all of the above myrmecophiles were found in a single large nest.

The relations of three ants found at various times in nests of *Formica obscuripes* are not clear.

Tapinoma sessile Say workers were found in the upper 3 or 4 inches (7-10 cm.) of what seemed to be a senescent *obscuripes* nest. The interior of the nest was damp, many of the twigs were moldy and gave off a musty odor, and the whole appearance of the nest was as if abandoned. These *sessile* workers were extremely timid and avoided the light. Below this top 3 or 4 inches (7-10 cm.) of the nest a number of rather sluggish *obscuripes* workers were found. A small but flourishing nest of *obscuripes* was 600 feet (183 m.) distant.

Live workers, males and deälated alpha and beta females of *Lasius latipes* Walsh were found in digging up an *obscuripes* nest at a depth of about two feet (61 cm.). They did not seem to be captive and were possibly an independent colony.

Workers of *Leptothorax hirticornis* Emery were frequently found in *obscuripes* nests. The following excerpts from my notes upon a *hirticornis* worker, collected with *obscuripes* workers and brood and kept together in an observation nest, may suggest its relationship:

"This ant, at the approach of the large workers, flattens out as much as possible though they never seem to notice it and even walk over it." And the same morning "a worker was observed to open its mandibles threateningly at the smaller ant in its path but without further sign of hostility." Then "a worker, coming upon the smaller ant, moved nervously around, seized it violently at the same time curving its abdomen and spraying it with formic acid. The *Formica* grasped the *Leptothrax* at different places and seemed desperately trying to kill it; . . . several other workers came up and displayed hostility to the smaller ant but could not interfere because of its small size and the larger size of its attacker. Finally, the worker released it, and it crawled off, apparently none the worse although its abdomen glistened from the formic acid." The next morning this *Leptothorax hirticornis* worker was found dead. One antenna was gone, the distal part of the abdomen was cut away, and the viscera had been removed.

(c). Ectoparasites. All the ectoparasites observed were mites. These were found to be common on the sexual forms of *obscuripes* as well as on the workers. The mites, identified by the United States National Museum, include:

Parasitidae. . . . On males, females, and workers from at least five nests.
Uropoda sp. . . . On males, females, and workers from at least three nests.
Tyroglyphidae. Hypopi or migratory nymphs on males from at least two nests.

The mites became abundant on ants kept in the laboratory; upon a queen kept for nine months I estimated that there were over 200 unidentified mites, distributed as follows:

Posterior surface of petiole entirely covered by mites (at least 10).
About 18 on dorsal surface of abdomen.
At least 14 on each side of abdomen.
More than 50 on ventral surface of abdomen.
About 14 on dorsal surface of thorax.
At least 10 on each side of thorax.
About 5 on ventral surface of thorax.
About 10 on dorsal surface of head.
About 5 on each mandible.
Several on margin of compound eyes.
About 18 on ventral surface of head, completely lining several sutures.
At least 5 on each leg.

The only place on the queen free from mites was the antennae. The ant was rather feeble and died five days later but, whether from the mites, lack of workers to care for it, or length of time kept, I cannot say.

A common position for the mites is on the legs. On a female *obscuripes* the sole mite present was on the tibia-tarsal joint of the left metathoracic leg. Such a position is common.

XV. RELATIONS WITH OTHER ANTS

A. RELATIONS WITH ANTS OF OTHER *Obscuripes* COLONIES

The two *obscuripes* nests most studied were 90 feet (27 m.) apart on opposite sides of a wolfberry patch. Both had paths extending fully ten feet (3 m.) towards each other through the bushes. When workers from one colony were dropped upon the other nest they were immediately seized and attacked.

It seems probable that these are typical relations and that workers from one colony are as hostile to workers of another as if they were entirely different ants.

B. RELATIONS WITH OTHER ANTS

The relations of *obscuripes* to other ants, as far as observed, are entirely hostile.

As mentioned before, ants of two other genera, *Lasius* and *Myrmica,* were found in *obscuripes* nests in a condition indicating their use as food. Only thoraces of workers of *Myrmica scabrinodis sabuleti* var. *americana* Weber (MS) were found in refuse chambers, but a male of the same *Myrmica* variety, deälated queens and a worker of *Lasius niger* var. *neoniger* Emery and workers of *Lasius umbratus mixtus* var. *aphidicola* Walsh were found entire or partially eaten.

XVI. COMPARATIVE ASPECTS

Our North American ant fauna is believed to have developed from forms migrating in preglacial times from Eurasia chiefly by way of Alaska (Wheeler, 1908, p. 407). Consequently we find the ant faunas of North America and Europe to be very similar. Furthermore, many of our most representative ants are merely varieties or subspecies of European species. Such an ant is *obscuripes,* a subspecies of the European *Formica rufa.*

The genus *Formica* is now found over the entire holarctic region. Its type species, *rufa,* parent stock of *obscuripes,* occurs from Siberia and the Caucasus throughout North and Middle Europe to Great Britain, south to the Pyrenees and southern Alps.

Mounds of the typical *rufa* are built of much the same materials and are of the same shape as those of our *obscuripes.* The numerous openings are similarly scattered over the whole surface of the mound. Donisthorpe (1927, p. 290) referring to *rufa* in Great Britain says: "This species nests in woods in shady places, in clearings, and on the borders of woods and forests—but also in the interior—on heaths and commons, but never far from trees, being more generally associated with fir trees, though it also occurs in oak, birch, and other woods. Forel states that in the Alps it is intimately connected with the fir trees, occurring as high as the last of these, but never higher." Nests of the subspecies *pratensis* pictured by Eidmann (1926) are in forests in rather shady situations contrasting with open exposures chosen by *obscuripes.* Indeed, the common German name of the several forms of *Formica rufa* is *die rote Waldameise,* or the red forest ant.

Yung, according to Wheeler (1910, p. 191), has found that the populations of *rufa* colonies vary from 19,933 to 93,694 individuals and that the population does not vary with the size of the mound. It seems probable, however, that in North Dakota *obscuripes* populations vary with the size of the mound, and have populations of somewhat smaller magnitudes.

The mounds of *rufa* nests are considerably larger than those of *obscuripes.* The average height, according to Donisthorpe (1927, p. 291), is about 3 feet (0.9 m.), fully twice as high as my highest *obscuripes* mound (18 inches or 46 cm.). He has recorded nests 5 feet high (1.5 m.) and a *rufa* nest pictured by Wheeler (1910) is 2.15 m. high.

The structure of the mound proper is apparently similar: "a large underground chamber, which is connected by galleries with other underground chambers and other parts of the nest" (Donisthorpe, 1927, p. 291).

The age of some of these European *rufa* mounds is known and gives an indication of the age our *obscuripes* nests may reach. Donisthorpe records a nest known to an observer for ten years, one known to himself for over twenty years, and one kept under observation by Forel for over forty years.

A comparison of the food of *obscuripes* and *rufa* is especially interesting.

Eidmann (1926) in studying the relations of *F. rufa pratensis* to the forests of Germany made many collections of the prey dragged to their mounds. His findings are similar to mine for *obscuripes*. Insects constituted the great bulk of their prey and belonged mostly to the same orders and families. These, represented in both of our collections, are: Hemiptera (Pentatomidae), Lepidoptera (Noctuidae), Coleoptera (Elateridae, Carabidae, Scarabaeidae, Coccinellidae, and Chrysomelidae), Hymenoptera (Formicidae), and Diptera (Asilidae and Syrphidae). A large proportion of the prey was coleopterous. On one occasion he collected a captured female *Lasius niger brunneus* Latr.: I found females and a worker of the North American representative, *Lasius niger* var. *neoniger* Emery, similarly used as food by *obscuripes*. He collected a very few Diplopoda and earthworms which were not found here as the prey of *obscuripes*.

Colony founding in *Formica rufa* has been observed by Donisthorpe (1927, p. 300). He saw a *rufa* female after "several fights with some of the workers" actually enter a *Formica fusca* nest. He has recorded a number of observations of his own and of others showing that the *rufa* queen may enter a *fusca* nest and be adopted by the workers. The *fusca* workers rear her brood, which eventually supplants them. In some cases the *rufa* queen decapitates the *fusca* queen. Sometimes the *rufa* queen selects a queenless *fusca* colony. Nests of *fusca* have been excavated in varying degrees of supplantation, some containing a *rufa* queen and *fusca* workers and brood, some with a *rufa* queen, *fusca* workers and both *rufa* and *fusca* brood, and others with a *rufa* queen, *fusca* workers and *rufa* brood.

Another method of colony formation is discussed by Donisthorpe (p. 292). "A certain proportion of a colony will emigrate and form a new nest with one or more queens, and a colony thus split is enabled to spread in the immediate vicinity where the conditions are favorable and the same, rather than to send off swarms to less favorable localities."

The only record of the actual mating of the sexes of which Donisthorpe was aware in 1927 was an observation made by himself in England in 1911 when he witnessed the coupling of the sexes. "A number of *rufa* males and females were seen flying about in a timber yard, running about on a large mound of sawdust in the hot mid-afternoon sunshine, flying off and settling on it, the males appearing to rise more easily than the females. Copulation took place on the mound; I never saw a single pair together in the air."

These observations on colony formation and mating of the parent stock, *rufa*, suggest strongly the methods whereby *obscuripes* colonies are founded. *Formica fusca* forms cover the range of *obscuripes* and it is very likely that *obscuripes* will be found to be a temporary parasite like its Palearctic congener.

XVII. SUMMARY

1. *Formica rufa obscuripes* Forel is a widespread ant of western North America, ranging from Illinois to the Pacific Coast states and from the western Canadian provinces to Texas. It is found throughout North Dakota from the Red River "Valley" to the Badlands.

2. The taxonomy of this ant has been confused. *Formica rufa obscuripes* Forel, *F. rufa aggerans* Wheeler, and *F. rufa obscuripes* var. *melanotica* Emery are here considered together as one form, *F. rufa obscuripes* Forel.

3. The climatic environment influences the activities of this ant in the following ways:

a. The climate of North Dakota is such that *obscuripes* is active from April to November.

b. The wide range of temperature from between —40°F. to —50°F. (—40°C. to —45°C.) to between 100°F. to 110°F. (38°C. to 43°C.) within the state is tolerated.

c. The ant thrives in regions of the state having an annual rainfall of 10 inches (25 cm.) and in regions having an annual rainfall of 30 inches (76 cm.).

d. Relative humidities below about 25% when coupled with temperatures above about 90°F. (32°C.) cause a suspension of activities. Low humidities and high temperature with direct sunshine also cause the ants to remain below the nest surface. They are somewhat active at temperatures close to freezing and at temperatures as high as 103°F. (39.4°C.), provided the humidity is moderate.

4. Plants are an important factor of the environment: as hosts of aphids tended by these ants; as the source of their nesting materials; and through phytophagous insects as the ultimate source of their food; as a menace to the nest when the vegetation is luxuriant, through encroachment.

5. *Formica obscuripes* establishes its colonies in paraboloidal thatch nests of about 8 inches (20 cm.) in height and two to four feet (60 to 120 cm.) in diameter with many underground chambers extending to a depth of nearly five feet (150 cm.). The presence of the ants and their brood has no effect upon the nest temperatures; any differences in temperature between the nest and its surroundings are due to the inherent nature of the thatch. The mounds are made of twigs, grass blades, and herb stems from the nearby plants. An important feature of the nest is a large brood chamber in the center of the thatch mound in which all the brood is kept together.

6. From a representative colony 16,481 workers were taken. An additional 500 may have escaped and the brood (cocoons and callows) probably numbered about 2,000. The population of this colony was thus about 19,000.

7. The natural food of *obscuripes* is derived mostly from two sources: insects and aphid secretions. Not the slightest evidence was found to suggest that this ant might use plants as food. Orthoptera formed about 26% of all insects taken, Lepidoptera about 22%, Coleoptera about 17%, Hemiptera and Homoptera about 12% each, Diptera about 9%, and Hymenoptera about 7%. Among the insects collected by the ants are such injurious forms as grasshoppers and leaf-hoppers. Three species of ants used as food were collected: females and a worker of *Lasius niger* var. *neoniger* Emery, workers of *Lasius umbratus mixtus* var. *aphidicola* Walsh and a male and parts of workers of *Myrmica scabrinodis sabuleti* var. *americana* Weber (MS).

The aphid, *Aphis symphoricarpi* Thos., is tended by *obscuripes*, generally when on the wolfberry, *Symphoricarpos occidentalis* Hook. The aphid, *Neothasmia populicola* (Thos.), is tended by *obscuripes* on *Populus tremuloides* Michx.; another aphid, *Bipersona* sp., is similarly tended on sagebrush, *Artemesia* spp. The secretions of the aphids probably constitute a very important source of food. The relations between the aphids and ants are apparently of mutual benefit, the ants affording some protection in return for food.

8. Many myremecophiles live with the colony. Adults and larval Coleoptera and noctuid larvae take advantage of the favorable soil chambers for hibernation or development. Staphylinid beetles and the ant, *Leptothorax hirticornis*, may possibly prey upon the brood or isolated workers. Mites are frequently ectoparasitic upon the adults.

9. *F. obscuripes* colonies, if distinctly separated, are hostile to one another and are hostile to other ants.

10. This ant resembles its European congeners in nest structure, choice of food, and probably in life history; it differs in size of nest, population, and nesting sites.

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LAKE DEVELOPMENT AND PLANT SUCCESSION IN VILAS COUNTY, WISCONSIN*

Part I. The medium hard water lakes

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* From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Report No. 60.

CONTENTS

INTRODUCTION

In Wisconsin, aquatic vegetation has been studied largely under the direction of the Wisconsin Geological and Natural History Survey with reference to its limnological value, and by the Wisconsin Economic Land Inventory Survey with particular reference to its economic importance to fish culture.

The first intensive ecological study made of water plants in Wisconsin was done by Denniston in 1912 (1922) on Lake Mendota. This is one of the larger lakes of the southern part of the state. It contains a variety of habitats and has very hard water. Denniston divided the lake into sections of natural units and the vegetation of each was studied and compared on a basis of specific abundance. Several years later Rickett (1922) studied Lake Mendota in detail on a quantitative basis using the same natural divisions outlined by Denniston. He attempted to determine the total amount of vegetation growing in the lake and to show its abundance on various types of soil and at various depths. He also outlines in some detail, the methods of obtaining samples, taking data, and recording results and the general methods used in the present paper were obtained there. Later Rickett (1924) investigated the aquatic vegetation of Green Lake, in Green Lake County, Wisconsin, using essentially the same methods as he had used in Lake Mendota. In this second paper he discusses more fully some of the problems of aquatic plant distribution and makes observations upon the character of the shore line. In these two hard water lakes of southern Wisconsin there are represented the general aquatic plant features of the southern part of the state.

In 1929 Fassett (1930) spent one week in northern Wisconsin in Vilas and Oneida counties making a floristic survey of nine lakes and lakelets. These range in their chemical characters from medium hard to very soft water and in their color from clear to dark. A classification of plant types roughly resembling that of Warming (1909) was suggested and the plants within nine lakes were briefly discussed.

Steenis (1931 and 1932), working under the direction of the Wisconsin Economic Land Inventory Survey, visited lakes of value to fish life in Sawyer, Douglas, and Langlade counties, collecting or recording the aquatic vegetation. In his reports he has followed the *growth form* classification of aquatic plants suggested by Fassett and has correlated his data with water chemistry. These studies have clearly brought out the fact that there are definite relationships between types of aquatic plant life and lake chemistry. They have also stressed the economic importance of the larger aquatic plants to fish.

In none of the above studies has there been any attention paid to dynamic ecology or the relationships between aquatic plant associations. This, as a subject, has not been considered intensively in the United States and very

few ecological papers are to be found that deal with specific plants in regard to the succession of aquatic vegetation. In Europe the problems of aquatic plant ecology have been more fully appreciated and valuable studies have been published (Pearsall 1918 and 1921).

During the summers of 1932, 1933, and 1934 an opportunity was presented the writer to investigate the ecology of a series of lakes in southern Vilas County, Wisconsin, under the direction of the Wisconsin Geological and Natural History Survey, with the object of determining the total plant crop in lakes ranging in development from early youth to old age. The

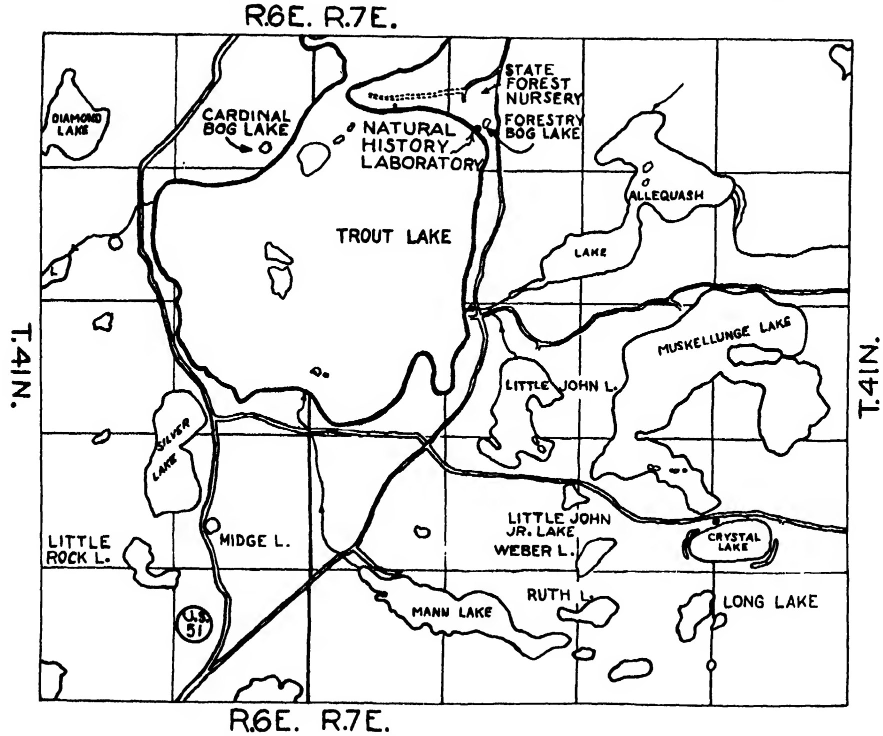

Fig. 1. General map of the region showing the location of lakes studied.

Highland Lake District of Wisconsin is particularly favorable for such ecologic studies because of the many lakes of wide range within easy access and the availability of chemical and physical data from the intensive limnological studies of Dr. E. A. Birge and Prof. C. Juday, also ample lake equipment and laboratory facilities are present (Juday and Birge 1930).

The area chosen for this study comprises about 27 square miles of Township 41 North in Ranges 6 and 7 East (Fig. 1). It contains numerous lakes of varied sizes and ecological conditions, which range from youth to old age. A series of lakes and lakelets were selected from this area that illustrate the development of a lake with its accompanied floristic history. Trout Lake

is omitted from the present paper because of its size and complexity. A detailed survey of the vegetation and shoreline has been made and the results show that though Trout Lake is the largest in the area, the problems of its ecology are like those of the others, and are probably more static due to its larger size. The series of lakes chosen are believed to be a true representation of the lake and floristic development within southern Vilas County and the adjacent regions of the same soils and glacial history.

PHYSIOGRAPHY AND SOILS

The physiography of southern Vilas County is definitely related to the Wisconsin Stage of glaciation and its topography varies with pitted and unpitted outwash plains, hills due to moraines and drumlins, and valleys, which lie between morainic features or are caused by glacial and postglacial drainage.

Beneath the glacial drift, Thwaites (1929) gives granite, gneiss and schist as the most important bed rocks and states that the relief of the bed rock surface is not very great. These rocks are essentially acid in nature and probably reflect to some degree that character in the soils of the region.

The importance of glacial activity in Vilas County is shown in the study of Thwaites, for in his discussion he makes the following statement: "The drift deposits of the area surveyed can be divided into (a) outwash, (b) terminal (recessional) moraines, (c) drumlins, (d) ground moraine, and (e) eskers. Of these, the first covers by far the largest portion of the region and the second forms the most conspicuous topographic features and the most striking country. The other features cover only an inconsequential percentage of the region."

Within the area here studied (Fig. 1) the irregular topography is due largely to the Muskellunge Moraine, ground moraine and glacial drainage, which resulted from the waters of the ice front as it rapidly melted. This moraine is very conspicuous in the southern portion of Township 41 of Range 7 and has been utilized as a location for a fire tower by the state forest service. Immediately to the north of the moraine much stagnant ice melted and formed outwash or deposited its load in the form of ground moraine, which also shows evidence of water working. The lakes were formed in depressions left by large masses of stagnant ice. The general history of the region is therefore quite simple, but the details of local conditions are often complex and are important in considering the distribution of soils. No attempt has been made to follow through the details of local glacial history of any lake except to determine the soil type and possible origin as it affects the ecological history.

The soils of the region have been studied by Whitson and Dunnewald (1915). The two most important mineral soils listed are Plainfield and Vilas in the soil series. According to Thwaites (l.c.) Plainfield soil originated from

outwash and is slightly weathered. Vilas soil is outwash with a few kames and some terminal moraine where the till is covered with a few feet of sand. It shows more alteration than the Plainfield soils.

Plainfield and Vilas soils are primarily sand and differ from one another in the quantity of gravel and sand. Each soil is divided into two or more types dependent upon texture, and the type of topography that it forms. The Plainfield soils are divided into the Sand and Fine Sand groups. Both of these are present in the area under discussion with the first as the more abundant. The Vilas soils are likewise separated into types but only the Sandy Loam phase is abundant and considered here. The two tables given below present a comparison of these two types of mineral soils. They are compiled from tables given by Whitson and Dunnewald and represent the extremes recorded by them.

Table 1. Mechanical analysis of soils in per cent

Soils	Gravel	Coarse Sand	Medium Sand	Fine Sand	Very Fine Sand	Silt	Clay
Vilas	5.75	11.74	13.84	25.64	15.25	15.08	5.75
Sandy Loam	11.73	12.59	13.91	26.54	16.04	19.30	6.60
Plainfield	2.54	14.57	21.20	27.08	4.71	4.75	3.34
Sand	9.10	22.44	30.30	37.37	9.87	9.61	9.92

Table 2. Chemical analysis of soil in per cent

Soils	Total Phosphorus	Total Potassium	Total Nitrogen
Vilas	0.041	1.20	0.030
Sandy Loam	0.064	1.57	0.103
Plainfield	0.027	0.87	0.025
Sand	0.052	1.36	0.096

The soils about and in each lake are variable and will be considered separately.

The drainage of the larger lakes of the area, as seen on the map, (Fig. 1), is into Trout Lake and thence to the Manitowish and Wisconsin rivers. If perfection of drainage be considered as an indicator of physiographic maturity, the region is in extreme youth. The processes of erosion have not perfected to any degree the drainage of Vilas County and consequently much of the former water area has developed into bog land.

THE DEVELOPMENT OF LAKES

In the subject of lake development two processes that have a profound influence on lake history and ecological conditions should be kept in mind. These are erosion and sedimentation. They are important in the development of an area to its base level, and if the climate is not too severe, the stage

to which these processes have succeeded is reflected in the vegetation of the region regardless of whether it is aquatic or terrestrial. Erosion as a process is continually at work carrying materials from higher to lower levels and cutting away the headwaters of gullies and river courses, thereby perfecting drainage. By this process materials both inorganic and organic reach their places of rest and are constantly filling up bodies of water and changing the chemical and physical characters of the lakes. In a region of physiographic youth, such as Vilas County, the drainage is very imperfect and sedimentation is the more active process. Because of the slowness of the erosional process in Vilas County, vast areas of water isolated from any drainage system will be filled with weathered peat soils by the time the region has reached maturity. Consequently erosion may be disregarded except where lakes receive a constant supply of mineral salts in the sediments which streams carry into them.

The developmental details of lakes from their origin and youth to old age and extinction is a subject that must be considered with regard to geography and geologic history of a specific region if minor generalities are to be determined. All the details of development of the lakes in Vilas County do not hold for those of southern Wisconsin or even eastern Langlade County, just 50 miles southeast, where the soils are largely derived from a limestone drift instead of sand and silt as is the condition in southern Vilas County.

A classification of Wisconsin lakes based on drainage has been in use for some years by the Wisconsin Geological and Natural History Survey. The lakes are separated into those which belong to a drainage system and those which are isolated from such a system. They are known as drainage and seepage lakes and by this simple division much can be predicted about the chemistry and physics of the water and a rough estimate of the physiographic age of a lake can be made. In a recent study (Juday and Birge, 1933) some chemical and physical characters of over five hundred Wisconsin lakes have been considered with reference to this classification. The investigation has shown that conductivity of lake waters is greater in lakes having regular drainage. The bound carbon dioxide content and hydrogen ion concentration are likewise higher in drainage lakes than in seepage lakes. These conditions seem to be retained by the constant influx of silt bearing water. From this study it is evident that the drainage lake is most likely to be the medium to hard water lake and the seepage lake the soft water lake. In using the terms hard, medium, and soft water the following scale used by the Wisconsin Geological and Natural History Survey is employed:

Soft....................	0-10 parts per million of bound carbon dioxide
Medium hard............	10-30 parts per million of bound carbon dioxide
Hard...................	over 30 parts per million of bound carbon dioxide

A deep lake in Vilas County, Wisconsin that remains part of a drainage system throughout its development, first becomes smooth in outline as the

bays fill with sediments and vegetation, and finally, swamp and bog. Further maturity is shown when sediments have filled the lake to a point where it is shallow enough for aquatic vegetation to cover nearly the entire bottom. Then a channel is developed and natural levees are formed on each side, while in back, swamp land and bog gradually form.

The stages in progressive development of a seepage lake, disregarding the specific vegetational history, is outlined in the following six steps.

(1) The lake becomes, or is originally, isolated from a drainage system.

(2) The bays are cut off from the main body of water by bars, spits, or ice pushes, forming across their mouths, and by the invasion of the land flora upon organic and inorganic sediments. The shape of the lake then becomes smooth in outline, often oval or round.

(3) Settling of the mineral salts, leaching of the mineral soils in the shallow water and around the lake, loss of electrolytes, bound carbon dioxide, and a decrease in hydrogen ion concentration.

(4) Organic sediments accumulate in sheltered places and in deeper water. There is an increase in water color.

(5) The invading land flora spreads about the perimeter of the lake developing mostly where it is sheltered from water movement, i.e., around logs, rocks, and sheltered sides of the lakes. The rapidity of further development depends upon the area, the depth, and the amount of debris blown or carried into the lake. The soils become organic.

(6) The land vegetation grows outward over the water until the area is covered by plants supported upon an organic mat. The shape of the lake again becomes irregular as it nears closure.

The Aquatic Vegetation and its Relation to Lake Types

A comparison between the terrestrial and aquatic vegetation of Vilas County shows each to have much in common with the other. The dominant vegetation of the region belongs to that of the Canadian Zone, while there are present in smaller quantities species of the Atlantic Coastal Plain flora, and terrestrial species of the western prairies.

The terrestrial flora can be divided, often very clearly, into two groups, one which grows on the rocky soils, called Vilas, and the other, on the sandy, called Plainfield soils. The climax trees found on the first are usually hard and soft maple, basswood, and white and yellow birch with the following conifers: hemlock, balsam fir, and red pine. The cut-over areas that now have a secondary growth upon them have an aspen, white birch and pin cherry cover. The climax trees of the Plainfield soils seem to have been white and red pine, but all that remains of most of these forests are large areas of stumpage. The secondary growth is dominantly aspen and white birch in the more moist places and jack pine in the dryer. The relation of soils and forest vegetation in the lake states region has been studied by Wilde (1933) and his

conclusions summarize the area of southern Vilas County very well. The Wisconsin Economic Land Inventory Survey under the direction of Bordner and Morris (1931) has mapped the cover of Vilas County and the vegetation is markedly related to the types of soil described by Whitson and Dunnwald.

The littoral flora of the region contains the usual Canadian species and also in a rather surprising abundance, species of the Atlantic Coastal Plain. Of these the more important are *Eriocaulon septangulare, Littorella americana, Juncus pelocarpus, Utricularia resupinata, U. cornuta, Rannuculus reptans, Dulichium arundinaceum,* and *Lycopodium inundatum.* The occurrence of these and others in the sand barrens of northwestern Wisconsin has been studied by McLaughlin (1932) and he concludes that their appearance in northwestern Wisconsin is associated with the Glacial Great Lakes. Just how the species found in Vilas County fit into the early history of the region is not clear. Their presence was not known when McLaughlin was working with this problem.

The aquatic vegetation likewise has its Coastal Plain element in some of the *Potamogetons,* but the stress upon aquatic vegetation in northern Wisconsin has not been so much on its history as on its *growth forms* and their distribution in the various types of lakes. The first to point out this relationship in Vilas County was Fassett (1930). He observed that a rosette type of vegetation was the dominant plant life of the soft sandy clear water lakes, and that in the more alkaline lakes the vegetation was more massive. The following *growth form* classification was constructed and in the nine lakes and lakelets in which observations were made there seemed to be some definite distribution of the four groups: (1) *Plants with long lax stems and flexuous leaves.* These species with the exception of *Utricularia* appeared to be restricted almost entirely to the more alkaline lakes of the region. (2) *Plants with stiff leaves in a close rosette or on short, rigid unbranched stems.* These species occurred more often in soft clear water lakes, but some species were also found in both bog lakes (soft water) and in the alkaline lakes. (3) *Plants with vegetative stem horizontal and the leaves mostly or entirely floating on the surface of the water.* Species of this growth form appear in all types of lakes. (4) *Plants with bases in the water and photosynthetic parts mostly or entirely emersed.* These species appeared only in lakes of medium hard water, which are the alkaline lakes of the region.

During succeeding seasons Steenis (1932, 1933) further investigated the lakes of northern Wisconsin, examining several hundred of them, and classifying the plants as was done by Fassett. He suggested a fifth class to include those species which float on the surface or sink to the bottom. These species appear to be restricted to the medium hard water lakes. The results are exceedingly interesting in the support they give to the *growth form* type of ecological classification for aquatic plants. His tables show, however, a transition of one plant form from one type of lake into another, especially if they

are examined with reference to definite species. This was not discussed by Steenis and no reference was made to dynamic conditions in lake ecology.

When the present work was begun the distinctiveness of the clear sandy outwash lakes was noted. Crystal Lake, one of those described by Fassett, belongs to this category and is one of the best examples of a lake having a rosette type of flora. Other lakes of this type were examined and additional species of plants belonging to other classes were encountered. These additional species usually occur in less abundance and in a part of the lake that is more mature than the larger portion. In further investigating the effect of lake maturity upon the vegetation it was found that certain species, such as *Sparganium angustifolium,* though often present in sandy clear water lakes was sparse until the lake or some portion of it had developed to the stage where organic sediment covered the mineral soil. When this stage had been reached, *Sparganium angustifolium* became abundant and some other species usually abundant in the clear sandy lakes were sparse or absent. Here it became clear that, though they may be classified on the basis of similarity of conditions, these lakes and their vegetation are dynamic things in which their sequence can be followed determining the ecological relationship of each species of plant to the other. The soft water lakes presented a fairly simple progressive series of stages, but when the medium hard water lakes were examined, perplexing problems were encountered. These problems when summarized centered largely about the types of sedimentation and the soils which resulted from them.

Frequently in portions of the medium hard water lakes, as in the soft water lakes, are found small areas with a distinctly different type of vegetation. Where sheltered bays exist sediments accumulate rapidly and the vegetation is often luxuriant and of the flexuous type. Where the soils are sandy and these have been leached to some extent there occur plants such as are typical of Crystal Lake. The extent to which these rosette or soft water lake species are found in a medium hard water lake appears to be the extent to which the lake, or portion of it, has become modified by the processes which produce such conditions. The question soon arose as to the source of the soft water vegetation, if it did not always exist in the lake. It is easy to account for the disappearance of a species from a lake by ecological succession but it was not clear from what source the new members were to come, if they had not previously existed there, at least in small quantities. An examination of the following important "rosette species" in the sandy clear water type of lake, suggests that *Lobelia Dortmanna, Eleocharis acicularis, Juncus pelocarpus, Gratiola aurea,* and several others, are derivatives from the beach zone. They are terrestrial plants that "go aquatic" when conditions in the lake become favorable. A detail study of this succession has been made and will be discussed at length with the soft water lakes.

METHODS

The methods used during 1932, 1933, and 1934 for the determination of plant quantities were essentially those developed by Rickett and described in his paper on Lake Mendota (1922). Several changes were made as the work progressed and a brief description of the methods are given here. In Lake Mendota and in Green Lake, Rickett collected plants from quadrates of one-half square meter by diving either with or without a hood. This was found impossible to follow in the Vilas County studies because the plants were found growing at greater depths, much beyond where a diving hood would be practical and also because the waters are too cold for extensive swimming during the entire season. Instead, a small modified Peterson dredge fitted with a heavy, calibrated, water-proofed, cotton rope was used to collect plants. This dredge is capable of denuding an area of 100 square inches or 625 square centimeters and at the same time of picking up enough soil to take specimens for laboratory examination. Another feature of this dredge is that it usually collects both roots and leafy stems making it possible to determine the entire plant crop and proportion of root and leafy stem. In the rosette type of vegetation the roots make up almost as much of the plant weight as those portions which occur above the soil.

When a lake to be studied was first visited its natural divisions were determined. Then the number of transects that were to be made through these was decided upon, though usually each division was small enough to make it unnecessary for more than one to be run. (See individual maps of the lakes studied). Where a shoreline is smooth in outline there is usually a uniform aquatic habitat to be found opposite it in the lake. Along such shorelines, especially where they cover considerable distance, transects were often made as checks upon one another.

A transect consists essentially in a profile study of the lake bottom from the shore into water beyond the outer limit of vegetation. This is made along a straight line usually through the middle of a natural ecological division in the lake. It consists of a series of quadrate collections beginning at one-fourth meter in the larger lakes and one-eighth meter in those which have vegetation in shallower water. Plants from successive quadrates were collected as the water deepened by one-fourth meter. Each collection of plants was washed free of debris in a screen especially constructed to hang over the end of the boat, and then they were packeted and labeled. Soil samples were not collected along every transect but only along those where new bottom features were encountered. The soils were carried to the laboratory in pint or gallon jars depending upon their nature, and dried by the sun in evaporating dishes.

At the laboratory the plant packets were divided into species and dried in the sun. Then each species collection was weighed and recorded.

The records consist of the air dry weights of each species from each station

and each depth at which it was collected. With this information it is possible to determine the optimum growing conditions of the various species when correlated with other studies made on the lake.

When these methods were first used in Vilas County they were tested in detail on Weber Lake (discussed in Part II). Transects were studied at intervals of about fifty meters entirely around this lake. When the results were graphed on depth and weight each species showed a remarkably smooth curve, bearing out the visual changes noticeable to anyone studying aquatic plants in this lake.

In determining the entire crop of each species in a lake the weight of all collections of that species were added together and the average weight per square meter determined. This was then multiplied by the total area colonized to determine its total crop in the lake. The area colonized by any one species was figured from the maximum depth. Such a computed area will naturally introduce some error of area, but this was corrected in part by dividing the natural divisions into two or more groups depending upon the depth of plant growth.

TABLE 3. Summary of lake characters

(From the records of the Wisc. Geol. and Nat. Hist. Surv.)

Lake	*Total Area* (sq. kilom.)	*Max. Depth* (meters)	*Color*	*Bound* CO_2 (pts. per Mil.)	*pH*	*Conductivity*
Silver	.87	19	0	14.3	7.6	59
			8	20.0	7.8	60
Muskellunge	3.72	21	8	9.0	6.6	38
			14	10.5	8.2	53
Little John	.67	6	14	8.34	6.8	68
			22	17.20	8.4	71
Green	11.90	68	4	37.8	8.1	275
			6			
Mendota	39.40	25	14	34.2	8.7	285

SILVER LAKE

Sections 23, 24, 25, and 26; Township 41 North; Range 6 East

As is true of all other lakes observed in the region, Silver Lake has developed in a kettle hole left by the retreating Wisconsin ice front. The lake, except for a constriction near its middle, is nearly oval in outline (Fig. 2). It is about one mile long, and about one-fourth of a mile wide. The total area is 872,000 square meters and the maximum depth is 19 meters.

The topography of the surrounding upland is hilly and rugged especially on the southern and western sides. There are present at the south end of the lake several large boulders and many smaller rocks. According to Thwaites (l. c. Fig. 1), Silver Lake is in an area of outwash. If this is true, the rugged topography and the abundance of boulders indicate this to be a very thin mantle over the ground moraine.

The original shape of the lake has been altered very little, and there is a high, smooth shoreline almost entirely around the lake. Several low places and irregularities were present when the lake was first formed and at these the following changes have taken place.

At the southeast corner of the lake the water originally extended into a small bay. Sediments carried by various agencies, especially longshore currents, have filled the mouth of this bay with sand. Ice action has caused

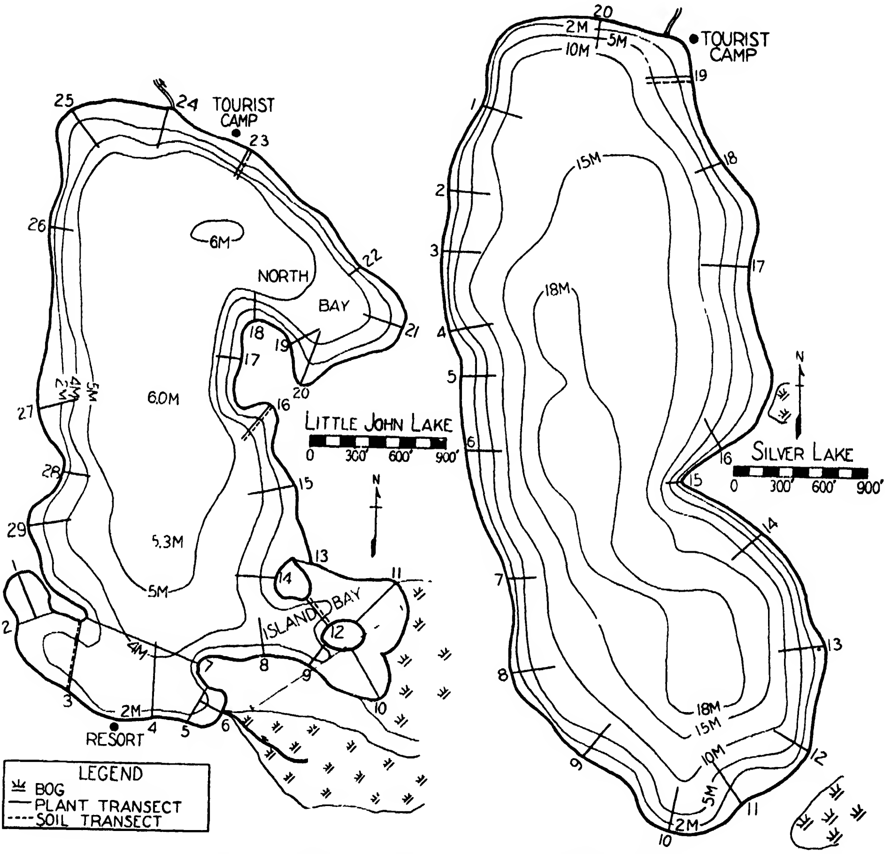

FIG. 2. Maps of Little John and Silver Lakes.

a ridge of sand to be pushed up, and this has permanently cut off the bay and smoothed the outline of the lake. This isolated bay has since become filled with peat and is now a *Chamaedaphne* bog.

A small point protruded on the east shore, near the middle of the lake, and on the north side of the point there was a small bay and what appears to have been an inlet channel. Sediments have collected in this bay and in the shallow water near the point. Ice activity pushed up ridges of sand and gravel, filled the bay and extended the point until at present it is more than 15 meters

longer than it was originally. There is evidence, by the presence of two very marked sandy ramparts, of two major extensions of this point. The development of the point has been such that its width was greater than the distance covered by the advancing ice from both sides of the point and consequently there is a low region between the ramparts that furnishes a habitat for a moist flora. The point has advanced into deep water and off the end there is a marked drop off.

At the northeast end of the lake there is a low portion in the shoreline through which the lake had its outlet. This flowed into Trout Lake. There also occurred considerable sedimentation of sand and gravel. This was pushed up into ridges by the ice and has blocked the outlet. Until the recent drop in lake level, the outlet stream has always been strong enough to erode through any ridge formed by the spring ice push, but at present there is an almost uniform sand and gravel rampart across the outlet and a natural resumption of this channel will be difficult unless there is a considerable increase in lake level.

Silver Lake at present must be classed as a seepage lake, though the outlet was functioning as recent as 1926. Prof. C. Juday observed it in use during 1902 and 1904. The frequency of the drainage when the lake was cutting its lower beach mark cannot be stated, but when the lake was at the level of a strongly developed beach, .7 of a meter above it, the drainage was continuous, and the outlet was probably a meandering stream, several meters wide.

The upper beach mark on the north side of the point is above the barrier which is across the old inlet, and it is certain that at its highest level the lake extended at least a short distance into the bay. At present, the whole inlet channel is filled with bog or swamp and no water appears to be entering the lake at this point.

The soils of the shallow water are either rocky or sandy and those of the deeper water are sandy until one reaches the ten meter depth, and then, in most parts of the lake, organic sediments are abundant. The upland soils have been mapped as Vilas Loam (Whitson and Dunnwald, 1915), and these are the soils that have been reworked by the lake water and quite regularly distributed as described above. In the southern portion of the lake a reddish sand or silt was frequently observed. This appeared to be a ferrous compound that had been deposited in a crust over the yellow sand in shallow water. The origin of this reddish soil seems to be associated with a bottom dwelling algae, but the formation of this material was not investigated.

The water of the lake is clear with little color or turbidity. Its color ranges from 0 to 8 and the conductivity from 59 to 60. The water is neutral to slightly alkaline with a pH of 7.6 to 7.8 and a bound carbon dioxide content ranging from 14.3 to 20.0 parts per million. With these properties, Silver Lake is well within the range of medium hard water lakes given above.

The very simple history of this lake is due largely to its original regular shape, steep embankments, relatively great depth, as compared with its area, and its sandy and rocky soils. For these reasons it has remained comparatively primitive and of the three lakes discussed, the sum total of youthful characters of Silver Lake appear to be greater than in the two others.

THE FLORA AND ITS DISTRIBUTION

Silver Lake contains fourteen species of vascular plants and one species of *Chara* (Table 4). These are species which occur in both the medium hard water lakes and in lakes of softer water. The latter species are less abundant than the former.

TABLE 4. Specific crops and their vertical distribution in Silver Lake

SPECIES	*Specific Crop* (kilograms)	*Percent of Crop* Zone I (0 to 1 meter)	Zone II (1 to 3 meters)	Zone III (3 to 8 meters)
Chara sp.	.09	35	65	0
Eleocharis acicularis	.23	67	33	0
E. palustris	5.15	100	0	0
Gratiola aurea, f. pusilla	.35	100	0	0
Isoetes macrospora	.62	78	22	2
Juncus pelocarpus, f. *submersus*	.41	97	3	0
Lobelia Dortmanna	.47	100	0	0
Najas flexilis	1.12	31	36	33
Polygonum natans, f. *genuinum*	1.34	100	0	0
Potamogeton amplifolius	.14	43	57	0
P. gramineus, var. *graminifolius*	3.14	59	37	4
P. pusillus	.08	8	16	76
P. Spirillus	.01	50	50	0
Ranunculus reptans, var. *ovalis*	.13	100	0	0
Vallisneria americana	3.79	19	46	35
Total crop	17.07	64	21	15

The total dry weight of plant life in Silver Lake is about 17 kilograms and for a lake of 872,000 square meters, this indicates a surprising sparseness. The total bottom area is only 23 percent colonized and much of this is bare sand. The greatest concentration of plants is in Zone I (0 to 1 meter). Here, 64 percent of the vegetation is found, while in Zone II (1 to 3 meters), 21 percent occurs and in Zone III (3 to 8 meters), 15 percent is present. In Zone I the greatest abundance of individuals is just below the line of wave action, which in most parts of the lake is seldom more than one-half meter below the surface. At this point there appears to be a deposition of organic debris and coarse silts that are washed from the sands of the shore and banks. In these sediments, the plants are comparatively more crowded than elsewhere in a vertical section.

Rickett (1922, 1924), divided the plant profile into three zones similar to that above, and though such a zonation is purely arbitrary it has a com-

parative value and in many cases covers the extreme ranges of natural units of the hydrophytic vegetation. For these reasons the system used by Rickett has been adopted.

The greatest depth at which plants were observed growing in Silver Lake was 6 meters. This occurred at Station 10, and the plants were *Potamogeton pusillus.* They were dwarfed and very slender, which would indicate that they were growing at their maximum depth. According to light transmission studies made on this lake (Table 6), only 6.8 percent of the total sunlight reaches 6 meters at a zenith sun, and the average amount is naturally much less.

Another instance where light penetration appears to be one of the main factors of plant distribution was found at Station 11. Here the water area is somewhat sheltered from the general wave disturbance of the lake and as a result a deposition of the finer silt and sand has taken place at a shallower depth than usual in Silver Lake. This type of sedimentation occurs as shallow as one meter and at this depth 62% of the total sunlight is present. Here the vegetation is massive and the dominant species is *Potamogeton amplifolius.* The vertical range of this species was found to be limited to the silted area between 1 and 1.75 meters. At the maximum depth the light intensity is slightly more than 40% of the total at zenith sun. A superficial analysis of the soils at other places in the lake show that the type noted at Station 11 frequently occurs in six or eight meters of water, but the light penetrating to this depth is less than seven percent.

On the north and west sides of Silver Lake the embankments are steep and are composed of a very rocky glacial drift. Generally the soils of shallow water are composed of rocks and gravel with occasional small pockets of sand. The rocks and gravel have accumulated near the shore and have formed a shelf. The plant life upon this shelf is sparse and composed largely of the bushy form of *Najas flexilis, P. Spirillus, Isoetes macrospora,* and *Chara* sp. The shelf seldom extends into water deeper than one meter and there a slight drop-off, sandy soils predominate. Here plants of *Vallisneria americana,* and *P. gramineus,* var. *graminifolius* occur in addition to those listed above. *Najas* attains more flexuous proportions in deeper water and is the most generally distributed species of plant in the lake. *Vallisneria* flowers abundantly in Silver Lake below the rocky shelf to a depth slightly more than two meters, and *P. gramineus,* var. *graminifolius* has been observed to produce fruit in water nearly three meters deep. Beyond three meters the plants of this species produce only under water leaves, and at its maximum depth of four meters, the plants are seldom more than a few centimeters in height. At four and one-half meters *Vallisneria* and *Najas* reach their maximum depths and these species form the sparse outer fringe of vegetation in the lake except at Station 10 where *P. pusillus* was present.

On the east and southeast sides of the lake there is usually a littoral or

beach flora present and this is also often the important vegetation of the first zone. The beach vegetation is developed best where the soils are sandy and free of rocks. Such conditions are most frequent on the east and southeastern shores of the lake. This is true because the shoreline is slightly more irregular, the water is shallower at a greater distance from the shore, and the banks for the most part are less steep than those of the west shore. Another factor causing the sedimentation of sand on the eastern shores may be the prevailing northwestern wind.

Eleocharis palustris is the most conspicuous plant upon the beach and it extends into .75 meters of water. This forms intermittent but often dense phalanxes over the wet sandy beach and into the water such as illustrated in Fig. 4 for Muskellunge Lake.

The same species, that are found beyond the rocky shelf described above, occur here in shallow water, growing between the rootstocks of *Eleocharis*. Where there is a mixture of gravel and sand on the beach *Eleocharis* is not abundant. Often it is absent and above the water line replaced by several species of *Carex* and *Juncus*, while below, the same species already listed remain. This species may also be associated with *Eleocharis acicularis*, *Equisetum limosum*, *Polygonum natans*, and *Typha latifolia* where the soils show a neutral or alkaline reaction.

The sandy soils in Silver Lake that are neutral or alkaline are usually found in water that is more than one-half meter deep or they are soils that are being continuously deposited by shore currents. Where the sandy soils are somewhat more fixed, such as they are at Station 16, they tend to become acid near the surface. An examination of the soils at Station 16 showed that those upon the beach were slightly acid at the surface, but one-half meter below they were decidedly neutral or alkaline. Soil or water samples from below the surface showed a higher pH and bound carbon-dioxide content than at the surface. The color of the surface sand is yellow to nearly white, but as one digs below it becomes a coffee brown in color, indicating an enrichment from the soil above. This same profile was found in shallow water and there appears to be a degradation of these lake soils such as is described by Wilde (1933) for those of forest and swampland. If the above condition of the soils may be taken to indicate a downward movement of water it might be suggested that the lake basin is a "perched water table", a feature supposedly not uncommon in glaciated regions, especially where the drift is of a sandy nature. The relationship of perched water tables (impervious saucer-like basins in or upon porous soils) to swamps has long been known, but whether this same feature may be found in a lake basin the size of Silver Lake is not known to the writer.

The same soil condition appears to be present where sediments are being deposited but the color of the soils is much more uniform throughout the profile. This may mean that degradation or leaching is going on here as well

as where the soils are somewhat more fixed, but here the upper soils are continuously being renewed by the action of shore currents. These latter soils are, for the present at least, designated as unleached, and those which show an acid nature and lighter color are designated as leached. Below, in the summary of plant communities in Silver Lake, are listed the plants which occur upon the unleached soils in the three zones. The leached sandy soil in Zone I is a phase developed from the unleached, and upon this former there gradually appears a distinct flora which in part seems to be a littoral derivative. This community is particularly well developed at Station 16 but rare at other places in Silver Lake. The relationships of these communities are indi-

Summary of Plant Communities in Silver Lake

PRIMITIVE LAKE

Zone I	Zone II	Zone III
rocks and sand (unleached)	sand, silt (unleached)	sand, silt (unleached)
Chara sp.	*Chara*	*Najas* (flexuous form)
Eleocharis acicularis	*E. acicularis*	*P. gramineus*, var. *graminifolius*
E. palustris	*Isoetes*	*P. pusillus*
Equisetum limosum	*Najas* (bushy and intermediate form)	*Vallisneria*
Isoetes macrospora	*P. amplifolius*	
Najas flexilis (bushy form)	*P. gramineus*, var. *graminifolius*	
Polygonum natans	*P. pusillus*	
Potamogeton amplifolius	*P. Spirillus*	
P. gramineus, var. *graminifolius*	*Vallisneria*	
P. Spirillus		
Typha latifolia		
Vallisneria americana		

sand (leached)
E. acicularis
Gratiola aurea, f. *pusilla*
Isoetes
Lobelia Dortmanna
Ranunculus reptans, f. *ovalis*

cated in the summary by connecting lines and they briefly indicate the trends and stages of aquatic plant succession. It will be noted, especially on comparison with the summary schemes of Muskellunge Lake and Little John Lake, that only a simple and comparatively young stage of ecological succession has been reached in Silver Lake. This is well in keeping with the simple geological history and primitive character of the lake.

During the three years (1932, 1933, and 1934) that observations were made upon Silver Lake there was a continual fall in the water level. This drop of water level was accompanied by distinct shoreline changes. The soils were redistributed and sand replaced gravel in many places. The vegetation

of the shore and shallow water likewise changed its aspect during the three years. The vegetation in Zone I, at Station 16, became poorer in plants of those species commonly associated with the leached soils. Near the outer fringe of these species, plants of *Najas*, *P. gramineus,* var. *graminifolius* and *Vallisneria* became more abundant and the soils appeared to be taking on more color. The observations on pH, however, showed little or no change in acidity for identically located soils during 1933 and 1934 but the soils of equal depths during those years were slightly more neutral in the autumn of 1934 than the previous year. This may also be partly due to the fall in water level and the consequent slight change in sedimentation. The significant principle illustrated here is that the plant succession had apparently reversed itself, at least, during the period when the lake level was dropping.

At Station 13 a small colony of *Typha latifolia* was observed in 1932. It contained six poorly developed and badly torn plants. This colony was restricted from spreading upon the shore away from the lake because of the dryness of the sand and the narrow beach, and mechanical activity of the waves prevented a lateral or lakeward extension of the colony. The occurrence of this species in such an unfavorable habitat appeared peculiar, especially because *Typha* is a comparatively rare plant in southern Vilas County and it occurs no place else on the lake or in the immediate vicinity. It did not appear to be a recent introduction for the plants all had very old rootstocks. It is probable that this colony was more extensive earlier in the history of the lake but due to the smoothing of the shoreline with the result that less and less protection from the waves was afforded the species, it neared extinction. This is further suggested by the fact that in this region *Typha* is associated with only the youngest of the seepage lakes or with permanent drainage lakes. During the fall of the water level this colony could spread lakeward and in three years the number of plants has increased from six to eighty-nine (Fig. 3).

In 1932, near Station 19, a small sand spit was forming off an irregularity of the shore. *Eleocharis palustris* became established upon this and bound the sand slightly. It extended over the edge of the spit and further protected it from wave destruction. As the sedimentation of sand was continued the spit was extended across the indentation of the shoreline and formed a bar. *Eleocharis* invaded this newly formed sand area and gave it further permanence. In back of the bar there remained a small lagoon in which *P. Spirillus* and *P. gramineus*, var. *graminifolius* were important species. In 1933 this lagoon did not contain as much water and both species of *Potamogeton* produced plants that were smaller than the previous year. *P. Spirillus* produced only the broad floating leaves. The next year the lagoon contained no water and sedges were rapidly invading the wet sand. Both species of *Potamogeton* were still present. *P. Spirillus* produced again

Fig. 3. *Typha latifolia* growing on sand in Silver Lake. In three years this colony has increased from six to eighty-nine plants. This is probably due to the fall in lake level and greater exposure of sandy beach.

Fig. 4. North end of Muskellunge Lake near Station 52 showing the relationship between *Eleocharis palustris* and the sedimentation of sand.

only the broad leaves, but they were thicker. *P. gramineus*, var. *graminifolius* had lost its characteristic linear lanceolate aquatic leaves and produced instead a few broad and rather leathery leaves which appeared to be well adapted to aerial conditions.

MUSKELLUNGE LAKE

Sections 15, 16, 22, 24, and 25, Township 41 North, Range 7 East

The basin in which Muskellunge Lake is located is roughly crescent-shaped. It was formed by several very large somewhat segmented masses of ice that melted in close proximity of one another. The area covered by this

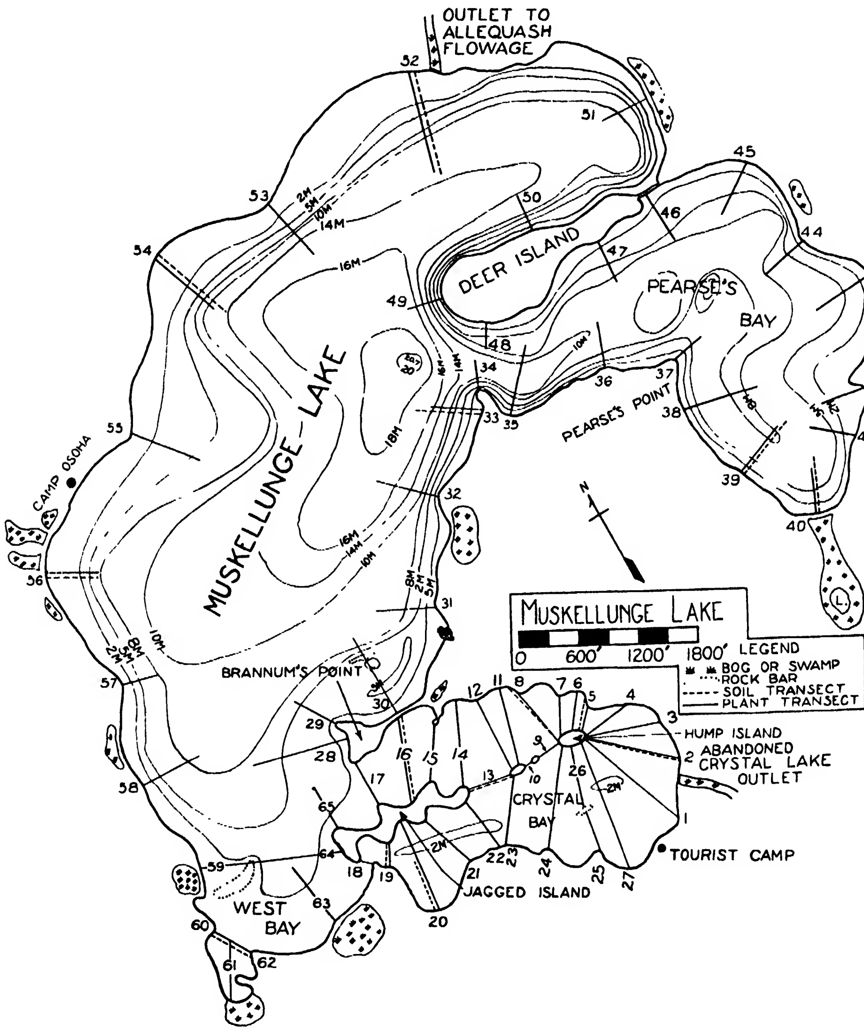

FIG. 5. Map of Muskellunge Lake

lake is 3,723,400 square meters and it has a maximum depth of 21 meters near the center of the lake between Stations 33 and 53 (Fig. 5).

In general the shoreline and the surrounding topography is high and morainic in appearance. There are also low places in the shore line that are now largely occupied by bog or swampland. From the melting ice

masses it is probable that there was considerable outwash. This seems to be a reasonable explanation for the flat areas of sand plain immediately to the south of the lake and on the southern part of the upland between the two ends of the crescent. Crystal and Weber Lakes (Fig. 1) are surrounded by clear crossbedded sand and these may owe their origin partly to outwash from ice in the Muskellunge Lake bed and region.

There are at the present time five islands which vary greatly in size. These occur in Crystal Bay and four of them form nearly a straight line from east to west across the bay. The fifth was a rocky reef, and appeared above the water in the summer of 1934 when the water level dropped .96 of a meter. This likewise has its long axis pointing east and west. The islands probably formed from materials that accumulated in glacial crevasses.

Other islands existed, but have either become joined to the mainland or to another island, or have been eroded to a level below the lake surface. Examples of the first type are Deer Island, and Brannum's Point; of the second, the west segment of Jagged Island; and of the third, the rocky reef through which the transect of Station 30 passes.

The original shape and area of Muskellunge Lake has been altered considerably since its formation. The tendency of the development has been towards a smoothing of the lake outline. This has been accomplished at numerous places, which is indicated in Fig. 5 as bog areas adjacent to the lake shore. The usual development at these places seems to have been first a sedimentation of sand at the mouth of each bay, and then this was pushed up into ridges across the openings. The isolation of the small bodies of water was followed by a rapid change in their aspect, and finally these have ended in being covered over by *Chamaedaphne* and other associated bog plants. One of these isolated bodies of water is still to be found at the end of Pearse's Bay. The portion isolated from Muskellunge Lake was more than 200 meters long and one hundred meters wide. There is a small lakelet near the center of the bog that has almost filled the former lake bed. The conditions which caused the isolation of so large a body of water seem to have been due largely to the narrowness of the lake at the place that is now the head of Pearse's Bay. The sediments carried by shore currents would naturally be deposited here and finally when these were near enough to the surface they were pushed up by the spring ice and a large body of water was isolated.

The soils in the shallow water of Muskellunge Lake are roughly of two types and it is possible upon this basis to separate the lake into two divisions. Crystal Bay and West Bay are shallow and the soils there are largely organic and for the most part, well decomposed. The second division constitutes the remaining part of the lake for there the soils are sand and gravel in the shallow water. The reason for this division is the marked difference in the general depth of the lake basin in these parts. Crystal Bay is formed in a comparatively shallow depression and the accumulation of organic sediments

has been rapid. In the open lake the general depth is increased greatly and these same sediments are seldom found in water shallower than five or six meters.

For a number of years Muskellunge Lake has not drained through the outlet at Station 52. This has been due to the progressive fall in the water level of the lakes of the region, and partly due to the formation of a sandy rampart across the mouth of the outlet. This latter is a common feature in northern Wisconsin and it undoubtedly has some importance in the isolation of a lake from its drainage system, and speeding up its future development. At present there is no known influx of water from streams or springs into Muskellunge Lake and consequently it must be considered as a seepage lake.

Early in the history of the lake there was an inlet between the transects of Stations 1 and 2. This stream flowed from Crystal Lake (see Fig. 1) into Muskellunge Lake, but for what length of time cannot be stated. At present there is an old sandy rampart more than 2 meters high across this channel on Crystal Lake, and on the shore of Muskellunge Lake there is also such a rampart though it is not as high. It is certain, from these observations, that the channel has not functioned at least for several centuries.

The fluctuation of the water level in Muskellunge Lake has been considerable since 1929. Measurements made at that time and in August 1934 show that the fall was approximately 1.1 meters. The result has been an exposure of a wide beach varying in width from 12 to 30 feet, and a redistribution of many soils especially those of an organic nature in shallow water. Bogs that formerly extended into the water were left high above, and in several instances the aquatic organic soils in front of the bog formation has been carried away and replaced by sand. Many of the plants in the bogs have died and are being replaced by an upland flora.

The mineral soils are like those of the upland in composition, and are of the Vilas and Plainfield types. These have been reworked into two general profiles illustrated by transects taken through Station 16 and Station 40.

In the first the maximum depth of the water is one meter. Samples of soil were secured from .2, .5, and .7 of a meter depth off the mainland and at the same depths off the north side of Jagged Island, and also half way between these points at one meter. Analysis of those soils near the mainland showed that at .2 of a meter the percentage of volatile matter present was less than 5%, at .5 of a meter, more than 10%, at .7 of a meter, about 25%, and at 1 meter, the percentage was nearly 70%. These same general results were found for the other samples though slightly less at each depth. Observations were made on the pH of the same samples and they were as follows for those near the mainland. At .2 of a meter the pH was 6.3, at .5 of a meter, 6.8, at .7 of a meter, 5.8, and at 1 meter the pH was 5.7. The other series of samples showed approximately the same reactions for identical depths. Samples

were not taken at the shore, because the soil there is composed only of coarse gravel (Fig. 6).

The analysis of the soils at Station 40 showed that there was only .52% volatile matter present at .2 of a meter, 1.77% at 1 meter, 1.29% at 3.5 meters, and 28.34% at 5.5 meters. The pH observations were made from the sandy beach above the wave limit into 8 meters of water. On the beach the pH was 5.0, but at the water line there was a rise to 7.0. Then at .2 of a meter, 5.8 was recorded and this was also found to be present at 1 meter. At 1.5 meters a slight rise was observed; at 2 meters the pH rose to 6.8, but at 4 meters another drop occurred and a pH of 6.0 was observed. At 6 meters the pH dropped still further to 5.8, where it remained constant as far down as observations were made.

FIG. 6. Crystal Bay in Muskellunge Lake from Station 15 showing a rocky spit formed by ice and wave activity. Part of Jagged Island is to be seen in the background.

This type of pH profile was encountered at every station where there were mineral soils present in the shallow water. The rise in pH at 2 meters and drop again at 4 meters at Station 40 was a surprising encounter, but this general curve appears to be the rule rather than the exception in the three lakes discussed. The depth at which the pH rises is very variable and may be determined by the amount of wave activity at each location. The soils of this profile as well as several others were tested with two different types of field pH indicator kits and the soils were also checked with a Quinhydrone apparatus. In all three instances the same curve was observed. A satisfactory explanation for this curve has not been found, but an examination of the soil types has suggested that the sandy soil upon the shore has a low pH because it is leached as already described. The rise in pH at the edge of the water may be due to the effect of phytoplankton that is constantly being washed

upon the shore. The drop in pH at .2 of a meter depth may be likewise due to a form of leaching accomplished by wave activity, and the greater this motion the greater may be the leaching. The point of rise in pH of the sandy soils may represent a depth below which leaching takes place. At this point there might be the beginning of a zone where there is still enough water movement to prohibit the deposition of the organic sediments that form lower down the profile and show an acid reaction. Associated with this pH curve there seems to be a rather definite distribution of plants, but this will be discussed below.

The water of Muskellunge lake is softer than that of Silver or Little John Lakes (Table No. 3). It is on the border line between the soft and medium hard water lakes and floristically it contains elements belonging to extremes of both.

Muskellunge Lake is an example of a lake tending toward the clear, sandy, soft water type in the open lake, while in Crystal Bay the trend is towards soft water and organic soils.

THE FLORA AND ITS DISTRIBUTION

The vascular plants of Muskellunge Lake number thirty species and the important species of algae are three in number (Table No. 5). These latter comprise of species, *Chara*, *Nitella*, and a species of *Nostoc*.

The dry weight of the total plant crop is about 882 kilograms. This grows on approximately 52% of the lake floor, and represents a much greater percentage of lake area covered by plants than in either of the other two lakes. This is true because Crystal Bay contains extensive crops over nearly its whole area and plants grow to greater depths in Muskellunge Lake than in the two others. Water shallow enough to produce plant life also comprises a greater percentage of the total area of the lake than in the other two described.

TABLE 5. Specific crops and their vertical distribution in Muskellunge Lake

SPECIES	*Specific Crop* (kilograms)	Percent of Crop: Zone I (0 to 1 meter)	Zone II (1 to 3 meters)	Zone III (3 to 8 meters)
Bidens Beckii	.76	72	28	0
Castalia odorata	219.91	97	3	0
Chara sp.	6.27	63	27	10
Elatine minima	trace	100	0	0
Eleocharis acicularis	8.18	87	13	0
E. palustris	23.26	100	0	0
Equisetum limosum	.12	100	0	0
Eriocaulon septangulare	148.82	100	0	0
Gratiola aurea, f. *pusilla*	.25	100	0	0
Isoetes macrospora	2.68	95	5	0
Juncus pelocarpus, f. *submersus*	2.30	100	0	0
Littorella americana	1.92	100	0	0

Species	Specific Crop (kilograms)	Percent of Crop Zone I (0 to 1 meter)	Zone II (1 to 3 meters)	Zone III (3 to 8 meters)
Lobelia Dortmanna	1.53	100	0	0
Myriophyllum alterniflorum	2.25	89	11	0
M. tenellum	13.29	73	27	0
Najas flexilis	2.95	41	54	5
Nitella sp.	155.20	0	1	99
Nostoc sp.	1.27	0	80	20
Nymphozanthus variegatus	23.01	100	0	0
Polygonum natans, f. *genuinum*	13.80	100	0	0
Potamogeton amplifolius	14.12	18	55	27
P. epihydrus	2.04	86	14	0
P. natans	1.02	100	0	0
P. gramineus, var. *graminifolius*	6.48	63	32	5
P. praelongus	23.16	61	39	0
P. pusillus	.66	0	67	33
P. Robbinsii	146.61	24	48	28
P. Spirillus	.06	50	50	0
Ranunculus reptans, var. *ovalis*	.76	100	0	0
Sagittaria gramineus	.76	100	0	0
Scirpus acutus	52.67	100	0	0
Sparganium angustifolium	3.06	99	1	0
Vallisneria americana	3.61	45	55	0
Total Crop	882.80	75	18	7

The maximum depth at which plants were found growing was seven meters. These were a species of *Nitella* that grows abundantly in Pearse's Bay. At seven meters the percent of the total sunlight at zenith is 4.4 (Table No. 6). The maximum vertical distribution of plants in Silver Lake was found to be six meters and there, 6.8 per cent of the total sunlight occurs. The plants observed at that depth were *P. pusillus*. This species was also found at a similar depth in Muskellunge Lake, and as in Silver Lake, 6.8% of the total sunlight is present at zenith.

Table 6. Percent of total sunlight at various depths in three lakes of Vilas County, Wisconsin

Depth (meters)	Silver*	Muskellunge†	Little John‡
1	62.0	62.0	20.0
2	38.0	40.0	12.8
3	26.0	26.0	4.0
4	17.0	16.0	
5	11.0	10.4	
6	6.8	6.8	
7	4.0	4.4	

* Birge and Juday (1932, p. 539).
† Birge and Juday (1932, p. 3?7).
‡ Birge, E. A. (personal communication).

The flora of Crystal Bay in Muskellunge Lake has been briefly described by Fassett (1930). The following excerpt from his report describes very well the condition in which the writer found this lake in 1932. "Muskellunge Lake, at least at the south end where visited by the writer, has very little shore vegetation. But in the water is a veritable jungle (Fig. 6). The flexuous-stemmed plants listed in table 1 are exceedingly abundant, as are the types with floating leaves listed in table 2. The short stemmed and rosette forms of table 2, while representing several species, are rare and localized." During the summer of 1932 there was noted a slight drop in the water level and there was an increase in the width of the sandy beach and likewise an increase in the rosette forms.

Early in 1933 this lake was studied intensely and the jungle-like vegetation noted by Fassett was found to be the most important element of Crystal Bay. The rosette forms, of which *Eriocaulon septangulare, Gratiola aurea,* f. *pusilla, Isoetes macrospora, Juncus pelocarpus,* f. *submersus, Littorella americana, Lobelia Dortmanna,* and *Myriophyllum tenellum* are the important species, were found to be common plants of the bay as well as the flexuous stemmed species. As the summer progressed and the water level dropped these species attained greater prominence in shallow water. These species listed above, with the exception of *Isoetes,* began to produce flowers as the water receded. The flowering of *Littorella americana* is considered to be a rare occurrence, and though this took place only at the water's edge upon the two smallest islands of Crystal Bay the abundance of the flowers made the narrow fringe purplish in color. In spite of the abundance of flowers and careful check that was kept upon them there apparently were no seeds produced. In 1934 this colony was entirely destroyed by the drought that lowered the lake level.

The species which constitute the jungle-like vegetation are *Bidens Beckii, Castalia odorata, Myriophyllum alterniflorum, Najas flexilis, Nymphozanthus variegatus, Polygonum natans,* f. *genuinum, Potamogeton amplifolius, P. epihydrus, P. natans, P. gramineus,* var. *graminifolius, P. praelongus, P. pusillus, P. Robbinsii, Scirpus acutus, Sparganium angustifolium,* and *Vallisneria americana.* This vegetation which in 1932 and 1933 covered much of the bay except in the channels between the islands, was reduced to about one-tenth of its former quantity in 1934. This was due to the drop in the water level of the lake and the redistribution of the organic soils. These completely smothered great areas of vegetation.

The small bay at the southwest end of the lake contains organic soils that are not as well decomposed as those in Crystal Bay. They contain much plant fibre and represent a type of raw peat. There the vegetation is more restricted in the number of species and the floating leaf type is the most abundant. The soils all show an acid reaction and the vegetation is also mostly of that type. The species typical of this habitat are *Castalia, Nym-*

SUMMARY OF PLANT COMMUNITIES IN MUSKELLUNGE LAKE

PRIMITIVE LAKE

ZONE I

rocks, sand, silt
(unleached)

Bidens Beckii
Castalia odorata
Chara sp.
Eleocharis acicularis
E. palustris
Equisetum limosum
Isoetes macrospora
Myriophyllum alterniflorum
M. tenellum
Najas flexilis (bushy form)
Nymphozanthus variegatus
Polygonum natans, f. *genuinum*
Potamogeton gramineus, var. *graminifolius*
P. natans
P. Spirillus
Sagittaria gramineus
Scirpus acutus
Vallisneria americana

sand, silt
(leached)

Castalia
Elatine minima
Eleocharis acicularis
Eriocaulon septangulare
Gratiola aurea, f. *pusilla*
Isoetes
Juncus pelocarpus, f. *submersus*
Littorella americana
Lobelia Dortmanna
Myriophyllum tenellum
Ranunculus reptans, var. *ovalis*
Sparganium angustifolium

organic soil
(partly decomposed)

Castalia
Elatine
Eleocharis acicularis
Eriocaulon
Gratiola
Isoetes
Juncus
Littorella
Lobelia
Nymphozanthus
P. natans
Sparganium

organic soil
(fiberous, "raw")
Castalia
Eriocaulon
Nymphozanthus
P. natans
Sparganium

Swamp and bog

ZONE II

rocks, sand, silt
(unleached)

Bidens
Chara sp.
Isoetes
Myriophyllum alterniflorum
M. tenellum
Najas (intermediate form)
Nitella sp.
Nostoc sp.
Potamogeton amplifolius
P. epihydrus
P. gramineus, var. *graminifolius*
P. praelongus
P. pusillus
P. Robbinsii
P. Spirillus
Vallisneria

organic soil
(well decomposed)

Bidens
Castalia
Chara sp.
Elatine
Eleocharis acicularis
Isoetes
Myriophyllum alterniflorum
Najas
Nitella sp.
Nostoc sp.
Nymphozanthus
Polygonum
Potamogeton amplifolius
P. epihydrus
P. gramineus, var. *graminifolius*
P. praelongus
P. pusillus
P. Robbinsii
Vallisneria

ZONE III

sand, silt
(unleached)

Chara
Najas (flexuous form)
Nitella sp.
Nostoc sp.
Potamogeton amplifolius
P. gramineus, var. *graminifolius*
P. pusillus
P. Robbinsii

organic soil
(well decomposed)

Najas
Nitella sp.
Nostoc sp.
Potamogeton amplifolius
P. pusillus
P. Robbinsii

phozanthus, P. natans, and *Sparganium.* In the open lake the vegetation belongs to the early phases of aquatic plant succession and indicates that Muskellunge Lake is a comparatively young body of water in this portion of its area. The dominant species of shallow water are *Isoetes, Myriophyllum tenellum, Najas, P. gramineus,* var. *graminifolius,* and *Vallisneria.* These are usually more abundant near the outer edge of the first zone. In deeper water, usually in Zone III, there is a change of the soils from sand to the well decomposed organic type. Upon these, *P. amplifolius, P. pusillus, P. Robbinsii,* and *Nitella* are often very abundant and form the outer fringe of the vegetation. The outermost member is usually *P. pusillus* or *Nitella* sp.

Pearse's Bay contains a vegetation that is quite different from the remainder of the lake in its abundance of deep water species. The most abundant form is *Nitella* and this occurs in enormous masses over the floor from about three meters to a depth of seven meters. *Potamogeton amplifolius* and *P. Robbinsii* are important species on organic soils to a depth of five meters. In this bay there was locally an abundance of *Nostoc,* a massive alga, that was often brought up to the surface in large quantities in the dredge.

In the shallow water at Station 40, the plants most frequently associated with sandy, acid soils were noted as occurring in the area of low pH described above, and those most commonly found upon the more alkaline soils occurred near the two meters depth where the soils showed a higher pH. How significant these observations are is not known at present, but there appears to be a definite relationship.

LITTLE JOHN LAKE

Sections 20 and 29, Township 41 North, Range 7 East

Little John Lake is a comparatively small body of water with 672,000 square meters of surface, a maximum depth of six meters, and an abundance of dissolved mineral salts in the water (Table No. 3). It has the hardest water of the three lakes discussed here, and it is a type of lake that is not very abundant in the region. The striking feature of this lake is its turbidity, which is due largely to the presence of great quantities of phytoplancton. These algae are abundant throughout most of the season of open water and give to the water a greenish yellow color during most of this time. Another feature of this type of lake is the abundance of well decomposed organic sediments in shallow water. These almost mask the mineral soils except where wave action is strongest. This type of lake has, as a rule, a steady influx of water, but during 1934 Little John Lake had much less than usual.

The topography in which Little John Lake is located is rough and morainic, except at the southern end, where there is a suggestion of local outwash plain. The basin of this lake has also resulted from the melting of an ice mass. The irregularity of the outline suggests that the mass of ice

was heavily loaded with glacial debris, and this is further emphasized by the fact that the lake is shallow with some irregularity upon its floor. This irregularity is most apparent at the southern end of the lake, but does not appear very plainly upon the map, for these features are intermediate between the contours.

The soils of the upland surrounding the lake on the west, north, and east are Vilas, Loamy Sand, and on the south the soil is Plainfield, Fine Sand. Much of the Vilas soil contains rocks and small boulders, and this, with the finer particles, makes up the mineral soil of the lake.

Along most of the shoreline except during high water, there is a narrow beach, which is rocky where the embankments contain the drift described above (Figure 7). At the north end of the lake extending from the transect of Station 25 (Fig. 2) to nearly that of Station 23, the history has been slightly different from the greater part of the open lake and here there is a well developed sandy beach during low water. At the head of each bay the shoreline is boggy where the plant life is encroaching upon the lake.

Two small islands are found in the southeastern part of the lake, where their presence has materially affected the sedimentation and plant life of Island Bay. Their origin is the morainic materials associated with ice as above described.

The original outline of the lake has been modified at the southeast, southwest, and northwest ends of the lake more than elsewhere. Near Station 6 there is an ice push across an inlet, but the scanty inflow of water is not prohibited, for it has eroded channels through the barrier. A large swamp extends up the valley along the stream course. This may have been partially filled with water, and possibly a part of the lake in its early history. At the head of Island Bay a swamp has formed and covers a considerable area that was formely the lake bed.

On the southwest side of the lake a point extends from the mainland more than one hundred meters. It is rocky and the construction shows that it was partly, if not wholly, built by ice pushing up ridges of sand, gravel, and rocks from the shallow water. These ridges are very marked near the end of this point.

The point on the eastern shore opposite, was not formed in the same manner, but is considerably higher and composed of rocky drift that has not been reworked by the lake waters.

At the northwest end of the lake, approximately the distance from the transect of Station 25 to a place half way between the transects of Stations 23 and 24, is a series of ice pushes, which form the shore embankment. This series has cut off a large portion of the early lake, and this was developed into a swamp land which contained, until recently a heavy growth of timber. Through the rampart the outlet has continued to flow, though this is usually

only during early spring and summer. When the lake was first studied the outlet was partially blocked by an old beaver dam, but recently this was torn out and a channel was dug through the debris. No effect on the late summer drainage has been accomplished.

In recent years there seems to have been very little ice activity in the lake, but in the past there must have been a great deal. This is suggested at Station 26 by old soil ramparts that were eleven feet above the lake level of 1934.

TABLE 7. Percentage of volatile matter in soils of Little John Lake

Depth in meters	Stations 3	16	23
0.5	——	2.31	.85
1.0	——	3.08	——
1.5	2.45	3.10	——
2.0	3.10	3.13	1.31
2.5	70.26	33.86	——
3.0			1.20
5.0			1.25

FIG. 7. The northwest end of Little John Lake from Station 27 showing the high banks which surround the greater part of the lake and the gravel and small stones that have been washed from the embankments.

The open part of the lake, because of its greater expanse and water movement, has remained more primitive than the bays. Sedimentation has been less rapid. The soils at Station 23 are quite typical of the open lake on a smooth shoreline and the percentage of volatile matter found in these is shown in Table No. 7. The volatile matter in the soils of Little John Lake appears to be largely of an organic nature, and their abundance might be taken to represent the speed of sedimentation. The remainder of these soils is silt, sand, and gravel, of which the most abundant mineral is quartz.

At Station 16 the effect of an undulating shoreline upon sedimentation of organic soil is well marked. Between 2 and 2.5 meters the change in the volatile materials is more than 30%, and physically the soil at 2.5 meters resembles that of the deep water.

In the bays except on exposed parts of the shoreline the soils are all of the organic type and are represented by Station 3 in the above table. The great abundance of volatile material at 2.5 meters is probably caused in part by the abundance of partly decomposed tissues of *Najas, Potamogeton,* and *Anacharis.* At Station 3 pH observations on the soils were made from the point toward the mainland and showed the following range: shore, pH 6.8; .2 meters, pH 6.0; .7 meters, 6.0; 1.5 meters, pH 5.3; 1.7 meters, pH 6.8; 2 meters, pH 5.9; 2.5 meters, pH 5.7.

The water of Little John Lake is higher than that of Silver or Muskellunge Lakes in its color, pH, and conductivity (Table No. 3), but the bound carbon dioxide content is slightly less than that of Silver Lake.

The water level of this lake has remained more constant than in the other two, but in 1934 there was a drop of .3 of a meter. This exposed much more sand and as the waves beat upon the shore they removed the finer sediments that had previously accumulated in shallow water. The lake became more youthful in the appearance of its shoreline.

THE FLORA AND ITS DISTRIBUTION

Little John Lake contains twelve species of vascular plants and a species of *Chara* (Table No. 8). They are forms found associated with the hardest waters of Wisconsin lakes and there are also a few forms that are abundant in the softest waters. These latter, however, constitute a minor part of the flora. The total area of the lake floor that is colonized by plants is but 31% of the whole, or 213,505 square meters.

The vegetation is largely concentrated into Zone I, and unlike the other lakes, there is a total absence of the larger aquatic plant life in Zone III.

TABLE 8. Specific crops and their vertical distribution in Little John Lake

SPECIES	*Specific Crop* (kilograms)	*Percent of Crop* Zone I (0 to 1 meter)	Zone II (1 to 3 meters)
Anacharis	2.52	0	100
Chara sp.	.61	88	12
Eleocharis acicularis	trace	100	0
E. palustris	4.31	100	0
Isoetes macrospora	trace	100	0
Myriophyllum tenellum	trace	100	0
Najas flexilis	78.03	61	39
Nymphozanthus variegatus	11.30	100	0
Potamogeton amplifolius	.20	100	0
P. gramineus, var. *graminifolius*	.04	100	0
P. pusillus	2.08	36	64

P. Richardsonii	12.56	83	17
Sparganium angustifolium	trace	100	0
Total crop	111.65	82	18

The total dry weight of the plant crop in Little John Lake is slightly more than 111 kilograms. The area covered by plants in this lake is almost the same as that covered by them in Silver Lake, yet the crop is nearly seven times as great. The average crop per square meter is .52 grams as compared with .08 of Silver Lake (Table No. 9).

The vegetation of the open lake may first be considered for it more nearly represents the early type of vegetation in Little John Lake. Here the most general and abundant species is *Najas flexilis.* It occurs in water that is from .2 to 3 meters deep growing on the sandy and rocky soils of shallow water and on the organic soil of deeper water. There is a general increase in abundance of this species as the soils become more organic and the water deepens to 1.5 meters. This seems to be due to the combined change in the soils and the lesser activity of the water at greater depths. *Najas flexilis* and *Potamogeton pussillus* grow to a depth of three meters. This is the maximum depth at which vegetation was observed. The reason for such a shallow colonization could not be determined, though several factors which might limit the downward distribution of plants are very pronounced in the lake. One factor, the turbidity of the water, may limit the amount of light which reaches below 3 meters to such an extent that plants cannot grow. Light measurements made by Dr. E. A. Birge (Table No. 6) on Little John Lake show that only 4% of the total sunlight reaches 3 meters at zenith. Readings with a six inch white disc were made on Little John Lake in August 1933 and give an indication of comparative transparency with that of Silver and Muskellunge Lakes. This disc was visible only to a depth of 2.2 meters in Little John Lake and in Silver Lake it is visible to a depth of 8.1 meters and to 5.2 meters in Müskellunge Lake. Another factor, that of rapid sedimentation of organic materials occurs below 3 meters in many parts of the open lake. At the lowest depths of plant colonization specimens were frequently found covered with a muddy deposit and they were apparently dying.

Other species occurring in the open lake and North Bay are *Potamogeton amplifolius, P. gramineus,* var. *graminifolius, P. pusillus, Sparganium angustifolium, Nymphozanthus variegatus,* and *Chara* sp.

Potamogeton amplifolius was found growing in abundance only at Station 20, in North Bay. The conditions there are not like those in the other bays, but resemble, with the exception of the shallow water (0 to 1 meter), the conditions of the open lake. *P. gramineus,* var. *graminifolius* was found only at Station 7 growing in sandy soil, while *P. Richardsonii,* and *P. pusillus* were generally distributed. *Sparganium angustifolium* and *Nymphozanthus variegatus* are not abundant in the open lake and grow only along the protected

shore of Stations 18 and 19. There, considerable organic soil has accumulated and this seems to be the reason for the appearance of these species.

Chara was found in considerable abundance at Stations 7 and 24, but was sparse at other places except in the bay at Station 3.

The bays are remarkably filled with vegetation, especially the small bay at the southwest end of the lake and the east end of Island Bay. Much difficulty was experienced in propelling a boat through the vegetation in these two bays and painted terrapins surprised while basking in the sun were often unable to escape through the floating mat. The beavers, which have a large house between the transects of Stations 9 and 10 have cleared runways through the tangle and these seem to be utilized by many other animals including terrapins and small fish. The plant that makes up almost the total crop in Island Bay is *Najas flexilis.* This species also makes up about four-fifths of the vegetation in the southwest bay. The ecological form of this species in the bays is the long lax type while in the open lake this form as well as the short bushy type is present.

The most primitive floristic condition of Little John Lake undoubtedly exists in the open lake where the shallow water soils are still sandy or only slightly covered by organic materials. Upon such soils plants of *Chara* sp., *Isoetes macrospora, Myriophyllum tenellum, Najas flexilis,* and *Potamogeton gramineus,* var. *graminifolius* grow. The first species is bushy or tree-like under such conditions as noted above. Chara is only sparsely present as is also *P. gramineus,* var. *graminifolius.* The lesser abundance of this last species in Little John Lake as compared with Silver and Muskellunge Lakes seems to be due to the greater abundance of organic soils in Little John Lake. If this is the reason for the comparatively lesser quantity then it seems reasonable to consider *P. gramineus,* var. *graminifolius* as colonizer of primitive soils and its little abundance an indicator of lake maturity. Wherever the water of the open lake is deep enough to allow the sedimentation of silt particles and some organic soils and not beyond the depth of other growing factors, *Potamogeton Richardsonii, P. amplifolius,* and *P. pusillus* may become abundant as in North Bay. When this habitat develops, *P. gramineus,* var. *graminifolius* disappears.

In 1932 *Isoetes macrospora* was collected only off the end of the point near the southwest end of the lake. Here it grew in water no deeper than in .2 of a meter. The soils were sandy and had a pH of 6.0. Two years later it was found to be slightly more abundant in the shallow water of Station 25. It was associated with *Eleocharis acicularis* and *Myriophyllum tenellum,* which are also members of the "rosette flora," characteristic of the soft water sandy lakes described by Fassett (1930). The occurrence of the last species was especially a surprise, for it is one of the most important members of the "rosette flora," and was considered to be a derivative of the beach zone. Instead it now appears, from the observations in this lake and several others,

to be a species similar in behavior to *P. gramineus,* var. *graminifolius.* However, it remains a member of a lake flora longer than the latter where a lake develops towards the soft, sandy, clear water type, or disappears earlier if the lake retains its hardness of water and develops into the type of lake which has an abundance of colloidal organic soil.

SUMMARY OF PLANT COMMUNITIES IN LITTLE JOHN LAKE

PRIMITIVE LAKE

ZONE I	ZONE II	ZONE III
rocks, sand, silt (unleached)	silt, organic soil (Unleached or well decomposed)	Organic soil (well decomposed)
Anacharis canadensis	*Anacharis*	No plants
Chara sp.	*Chara* sp.	
Eleocharis acicularis	*Najas* (slender form)	
E. palustris	*P. pusillus*	
Isoetes macrospora	*P. Richardsonii*	
Myriophyllum tenellum		
Najas flexilis (bushy form)		
Nymphozanthus varigatus		
Potamogeton gramineus, var. *graminifolius*		
P. Richardsonii		

silt, organic soil
(well decomposed)

Anacharis
Chara
Najas (slender form)
Nymphozanthus
P. amplifolius
P. pusillus
P. Richardsonii

organic soil
(not well decomposed)

Sparganium augustifolium
Nymphozanthus

Swamp and bog

The two southernmost bays and Island Bay present examples of rapid sedimentation and its effect upon the vegetation. The areas of these bays are small enough to be almost always free from rough water and consequently the sedimentation is rapid. There seems to be three sources of these sediments, (1) from the decay of an abundant vegetation in the bays (2) from organic materials blown into the lake, and (3) from sediments from the main part of the lake carried by shore currents and dropped in the still water of the bays.

At the head of each one of the bays small *Chamaedaphne* bogs are developing. These are encroaching slowly upon the water in back of a narrow zone of *Carex*. Out in front of these bogs there seems to be a more rapid sedimentation in process. The particles which make up the sediments are larger than those of deeper water and contain more fiber. These are apparently the transition sediments into what is commonly known as raw peat. The plants inhabiting these soils are *Sparganium angustifolium* and *Nymphozanthus variegatus*. They represent species that belong to the end of the aquatic plant succession series in Little John Lake. The following scheme summarizes the plant communities in Little John Lake and indicates their relationships.

A COMPARISON OF THE MEDIUM HARD WATER LAKES OF SOUTHERN VILAS COUNTY, WITH TWO HARD WATER LAKES OF SOUTHERN WISCONSIN

To compare those lakes of southern Vilas County that are described above, with the two hard water lakes of southern Wisconsin, that have been studied in the same manner, a brief discussion of the regions and their dissimilarities is necessary. A fundamental difference in the two regions is at once apparent in the bed rock of each. Whether this is the prime difference and the factor which governs the many other features, cannot be definitely stated. However, the granite and gneiss rocks of Vilas County are covered with a mantel of sand and other soils relatively poor in plant nutrients, while the localities in which Green Lake, and Lake Mendota are present the bed rock is limestone and the soils are relatively rich in the available bases so important to the growth of most plant life.

Both regions are located within the area of Wisconsin drift, but the nature of this drift differs in various parts of the state. That of southern Vilas County is essentially sand and gravel, and in the part of southern Wisconsin under discussion the drift is essentially clay, silt, and gravel. In short, one is a region of acid soils, and the other a region of alkaline soils. The glaciation of northern Wisconsin is more recent than in southern Wisconsin and the natural perfection of the drainage is completed to a much lesser degree.

As stated before, the lakes of southern Vilas County are developed in depressions left by the melting of the last ice sheet, but in contrast to these, the two southern lakes occupy depressions in limestone bed rock. The derivation of dissolved minerals in the waters of the southern lakes is from the sediments of streams flowing over the limestone drift and from the mechanical and chemical weathering of the rocky lake cliffs. The streams of Vilas County in contrast, flow over an acid drift and carry a comparatively small amount of mineral plant nutrients in their loads. There are no rock

or soil lake cliffs and as stated elsewhere, there is at present no very great influx of water into these lakes.

With such striking regional and physiographic differences as shown by the areas of northern and southern Wisconsin, it is logical to expect that there will be a vast difference in the water mineral content of the two regions. This expectation is confirmed by conductivity measurements upon the waters of these lakes (Table No. 3). The highest reading of conductivity in the three northern lakes under discussion was made in Little John Lake. This reading shows the conductivity to be less than one-fourth as much as is found in Lake Mendota.

The original soils of the three northern lakes are predominantly sand while those of Green Lake and Lake Mendota contain more clay and silt than sand. Those soils that have developed in the bays and below the depths of wave activity in the northern lakes are largely organic and vary from a colloidal, well decomposed type to raw acid peat. In Lake Mendota and Green Lake, these secondary soils are also partly colloidal and peaty, and in addition, large quantities of marl are present. There appears to be a difference between the colloidal soils of the soft and medium hard water lakes and those of the hard water lakes, but what that difference is, has not been determined. There is still much to be learned about aquatic soils.

A study of the lake areas and depths brings out another difference which influences a comparison based on plant abundance (Table No. 3). The smallest of the northern lakes is .67 square kilometers in area and its maximum depth is about 6 meters. The largest northern lake (Muskellunge Lake) is 3.72 square kilometers in area and has a maximum depth of 21 meters. Comparing these figures with Lake Mendota, the larger southern lake, it is evident that the latter is more than ten times larger than the largest of the three northern lakes, while in depth it exceeds Muskellunge Lake by only four meters. Green Lake is a little more than three times the area of Muskellunge Lake, but in maximum depth Green Lake is more than three times deeper than it or Lake Mendota. The relationship between area and depth in a lake as related to plant life is a variable feature and there is no general rule that can be stated. It is however, reasonable to expect a proportionately greater abundance of plant life as the area increases in a lake of irregular outline than in a lake of smooth outline. With the comparative increase of depth in lakes, plant life may become scarcer, if there is as a result, an absence of shelves or bars upon which it can grow. Upon the steeper slopes of the lake bed, fine sediments do not usually become fixed and plant succession is much slower on these areas. The vegetation of the five lakes is similar in the majority of species, but the northern lakes contain a dominant element in their flora that produces less tissue than that in the two southern lakes. This is the second type listed by Fassett in the *growth form* classification already discussed. A small lake, such as Little John or Silver,

that has a limited range of soils will usually contain a limited flora of larger aquatics. These lakes contain twelve and fifteen species respectively. Muskellunge Lake contains a variety of soils and habitat conditions and a flora of thirty-three species. Rickett (1922, 1924) has recorded twenty-one species for Lake Mendota and twenty-seven for Green Lake. In the latter he has listed a number of algae. These also occur in Lake Mendota. A comparison of the algae flora in the two regions has not been made, but it may be generally stated that in the soft and medium hard water lakes of northern Wisconsin, especially those that are clear and have sandy soils, the quantity of attached algae is considerably less than in the two southern Wisconsin lakes. In the lakes of Vilas County *Cladophora* was not encountered, but this alga is an important plant in Lake Mendota and is also present in Green Lake. Only once has the writer seen filamentous algae abundant in the lakes of Vilas County. This was present in the northwest end of Allequash Lake (see general map, Fig. 1) in late August, 1933. The alga, a species of *Spirogyra,* formed mats several inches thick and covered acres of water surface. It was

TABLE 9. A comparison of the colonized area and plant abundance of five Wisconsin lakes

LAKE	*Area Colonized* (hectares)	*Total Crop* (kilograms)	*Average Crop per sq. m.* (grams)
Silver	20	17	.08
Muskellunge	193	882	.45
Little John	21	111	.52
Green	857	1,527,900	178.00
Mendota	1,040	2,100,000	202.00

buoyed up by pockets of gas and was a bright yellow color. The only alga other than *Chara* and *Nitella* that was large and abundant enough to be considered in these studies was a species of *Nostoc* in Pearse's Bay of Muskellunge Lake. This alga was localized to that portion of the lake.

The total crops of the five lakes show a surprising range of productivity. These are compared in Table No. 9 and show their relationship to the area colonized by the plants in the respective lakes, also the average crop per square meter.

The much greater weight of plant life in the two southern lakes stand out as markedly as do the other comparisons already made. The explanation for such great difference of plant weight in the two regions appears to be the following: (1) sandy soils predominate in the north while silt and clay are more abundant in the south, (2) there is greater bulk of tissue in the dominant species of the southern lakes, and (3) there are also greater areas of lake bottom covered by the plants in these lakes. Another factor, that of temperature, may have some effect on the abundance of the crop.

In the northern lakes especially, but also in the southern lakes, it appears as though one might take the conductivity of the lake waters as an indicator

of the abundance of plant crop present in a specific lake. This indicator, however, appears to have limitations where marl is present in great quantities, for often in such lakes there is almost an absence of aquatic vegetation except where inlets enter.

The vertical distribution of plants in the five lakes show great variation in the percentage of the total crops in the three zones (Table No. 10), but the number of factors, which determine this distribution will not permit a general statement with the data now at hand.

TABLE 10. Comparison of total plant abundance in percent of whole crops

LAKE	Zone I (0 to 1m.)	Zone II (1 to 3m.)	Zone III (3 to 8m.)
Silver	64	21	15
Muskellunge	75	48	7
Little John	79	21	0
Mendota*	30	45	25
Green*	9	40	51

The total absence of vegetation in Zone III of Little John Lake has been suggested as due to the rapid sedimentation of organic soils, and the turbidity of the water, which does not permit a sufficient amount of light for the larger aquatic plants in this zone. In contrast to this absence of plant life in Zone III of Little John Lake is the occurrence of 51% of the total crop of vegetation of Green Lake below the three meters depth. The great bulk of this crop according to Rickett (1924) is made up of *Chara*. This plant is commonly found in enormous quantities and would naturally have marked effect on profile studies.

SUMMARY

1. In a series of medium hard and soft water lakes of southern Vilas County, Wisconsin the ecological factors and vegetation have been investigated on a quantitative basis. The results have been divided into two parts, Part I, the medium hard water lakes, and Part II, the soft water lakes.

2. The physiography of southern Vilas County and its history are discussed with reference to its effect upon lake ecology, the vegetation of the region, and the lake development.

3. The medium hard water lakes of the region contain the most complex studies and the three lakes here discussed present a typical cross section of these problems.

4. The abundance of each plant species was determined from dry weight by denuding quadrates located along profiles through natural ecological divisions in the lakes. Soils from each quadrate were correlated with plant crop, slope of the lake basin, and water movement.

5. Soils of a colloidal organic type found in comparatively shallow water in drainage lakes support the greatest abundance of vegetation while sand supports the least.

* From Rickett (1924).

6. The effect of light on plant distribution is apparent, but these records are still too incomplete to draw any conclusions from field observations.

7. A comparison of the plant life is made between two lakes of southern Wisconsin and three of Vilas County. A comparatively scanty crop in the northern lakes is explained by, (1) the dominance of sandy soils in these lakes, (2) the greater bulk of tissue in the dorminant species present in the southern lakes, and (3) greater areas are covered by the plants in two lakes of southern Wisconsin.

8. Marked plant succession in the medium hard water lakes of southern Vilas County takes place only where there is some active hydrographic process at work. Where these processes cause isolation from drainage the trend is toward a soft water plant community, but where the influx of mineral salts is not checked the succession is dependent upon the type of soil which accumulates.

9. The relationship between aquatic plant communities in three lakes has been graphically determined from a study of the specific abundance on various soils, and at various depths in these lakes. The general scheme of aquatic plant succession in southern Vilas County, Wisconsin is being reserved for Part II, after the soft water lakes have been discussed.

The writer wishes to express his appreciation to the Wisconsin Geological and Natural History Survey for the opportunity and facilities for studying the problems of lake ecology in the Highland Lake District of Wisconsin, and particularly to Dr. E. A. Birge and to Prof. Chauncey Juday for valuable advice and discussion during the direction of the work. Acknowledgment is due to Dr. N. C. Fassett of the Department of Botany, University of Wiscon sin, for checking the identity of aquatic plant species belonging to technical genera and for numerous suggestions and criticism. For invaluable assistance in the field and in the reading of the manuscript, the writer is indebted to Mrs. L. R. Wilson.

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ECOLOGICAL MONOGRAPHS

VOL. 5 JULY, 1935 No. 3

SOME MARINE BIOTIC COMMUNITIES OF THE PACIFIC COAST OF NORTH AMERICA[1]

PART I. GENERAL SURVEY OF THE COMMUNITIES

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PART II. A STUDY OF THE COMMUNITIES OF A RESTRICTED AREA OF SOFT BOTTOM IN SAN JUAN CHANNEL

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[1] Contributions from the Zoological Laboratory of the University of Illinois, No. 467.

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By V. E. Shelford

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By V. E. Shelford

Part II

A Study of the Animal Communities of a Restricted Area of Soft Bottom in the San Juan Channel

By Nettie M. Wismer, Lawrence (Kansas) High School and John H. Swanson, Edinburgh College

Part I

GENERAL SURVEY OF THE COMMUNITIES—THEIR EXTENT AND DYNAMICS

The Major Communities

By

V. E. Shelford

I. Introduction

In 1925, Shelford and Towler published a brief description of the marine communities near the Puget Sound Biological Station (now the Oceanographic Laboratories of the University of Washington). Data as to the physical and chemical conditions and the depth and bottom were summarized. This study considered about 75 km^2 of the 1000 km^2 covered in the investigations and reconnaissances which form the basis for the discussion in this paper. Our primary object in this monograph is to describe several new communities. One of them is a community of major or formational rank resembling those described by Petersen and colleagues ('11, etc.), and covers about one-fifth the sea bottom discussed. Its larger features were investigated in the summer of 1926, 1928 and 1930 by Shelford, while Weese undertook a special study of East Sound and Olga Bay in 1929. There was a sufficient overlapping of the stations of these two investigators to facilitate coöperation and comparison. This major community with its variations and subdivisions illuminates various important problems concerning the significance of physical factors and the reactions of organisms on the habitat.

As the investigation was extended to cover a larger area several subdivisions, and variations of the communities described in 1925, were discovered. The knowledge of dominant and influent animals, especially the motile forms, was extended and a revision of the lists of characteristic, uniformly distributed and important species was rendered necessary. The selection of representative species to illustrate general principles is difficult because of a lack of knowledge of habits and life histories and especially of variations in abundance from year to year. In a community such as the Strongylocentrotus-Argobuccinum biome,[2] briefly described in 1925, there are many important species. While a much longer list is presented here than in 1925, a still larger list would be desirable as many common forms receive no attention because they are not abundant or are not properly identified. The adequacy of the data for purposes of general discussion is, however, greatly extended over that of 1925.

[2] Biotic Formation.

The work of Weese on the faciations[3] of the new major community (Pandora-Yoldia biome) indicates the way in which physiographic processes may bring about a complete change in conditions and communities and thereby a complete change in fossilizable forms, the causes being entirely local and capable of taking place within a very short period. The work of MacLean carries the series of communities described by Weese farther toward the land climax of the region.

Rice's work on the Balanus-Littorina community serves a timely purpose of indicating the significance of the peculiar arrangement of individuals in various places. Her observations in southern California in 1931 although not presented in this paper served as a check on the observations of Rasmussen and those published by Shelford ('30). Observation on the tidal communities (Balanus-Littorina) at Barkley Sound (west shore of Vancouver Is.) has further illuminated the question of peculiar arrangements of species.

The actual investigations were supplemented by the general knowledge gained by dredging, bottom sampling, seining and clam digging, as well as other operations with classes of graduate students. Twenty or thirty graduate students were able to handle large amounts of material. This was done in a systematic and orderly way. For example, clams were dug on contour lines determined with a transit. The work was carried on in all cases with the aid of an assistant thoroughly familiar with the fauna. The discussion of the new Pandora-Yoldia biome and most of the other communities, is, however, primarily based upon investigations conducted for that purpose. The work of Wismer and Swanson (page 333) deals with the communities of soft bottom in a primarily hard bottom community area. While their work was done in coöperation with the other studies it constitutes a separate unit.

The communities are graded with reference to what are supposed to be the *largest community units* of the same or similar taxonomic composition. Since investigations have not as yet shown the extent of these larger units or their degree of fragmentation, the classification must be regarded as subject to revision, especially as regards leading dominants of uniform distribution throughout any major community (including its various fragments). The largest communities are distinguished by a *difference* in essentially *all* the species of abundance or dominance. The general plan of community classification adopted by American and British plant ecologists has been applied. Deviation from their familiar terms and usages are explained where such terms are used.

The experimental work of the writer and his associates, and life history studies of investigators at the station have been given community evaluation.

[3] The term faciation is applied to modification of the association resulting from the loss or the addition of a few of the important species.

This is limited, however, to studies concerned with species important in communities or studies having a general bearing upon the physiological differences between communities.

Two new methods were employed quite generally, especially in connection with the work on the new major community; the description of the implements used, particularly of a new quantitative net, is a further purpose of this paper. A much greater refinement in all the methods used as compared with the 1925 work has been possible in connection with the study of all the other communities of the area.

II. AREA OF STUDY, METHODS AND COMMUNITIES

1. AREA OF STUDY

The area of study of the work of Shelford and Towler ('25) has been extended principally to the north and east. The northern boundary of the area which has been included in the investigations and reconnaissances is approximately 48° 48′ N. passing just north of the island of Patos. On the south, the southern end of Lopez Island, 48° 25′ N. is the boundary. The area is indicated in Fig. 1, and comprises approximately 1000 km^2, or 386 sq. mi. of water.

Approximately thirty-five dredging and bottom sampling stations were used and are indicated in Fig. 1 and 1a (nos. 51-85; 85 is shown on insert map). Stations 63 to 75 were intensively studied due to the presence of a series of communities hitherto undescribed, which occur on mud bottom in 3-75m of water in protected bays.

Other newly investigated bottoms were rock, sand, and mud in Rosario Straits, Barkley Sound, and Guemes and President Channels. Approximately 225 meters at Station 56 was the greatest depth reached with dredge or bottom sampler. For comparison a study was made by Shelford at Barkley Sound (west coast of Vancouver Island) covering several communities in some detail and significant reconnaissance of the shallow water bottom communities was also made. Use was made of observations on other parts of the Pacific Coast. On rocky shores between tide lines twenty-five stations indicated by a circle and arrow in Fig. 1 (1-25; 22-25 are shown on the insert map) were used for the study of barnacle-mussel communities. Fifteen stations were devoted to the study of bivalve-worm communities when exposed at low tide. They are indicated by a square and arrow in Fig. 1.

The general conditions in and about San Juan Islands were discussed by Shelford and Towler ('25). Since that date considerable investigation of the water from the chemical standpoint has been conducted by Thomas G. Thompson and his associates. Such studies include determinations of oxygen and salinity. Fig. 1 shows the salinity as indicated by isohalines. The map covers a larger area than the map already published (Shelford '30). The

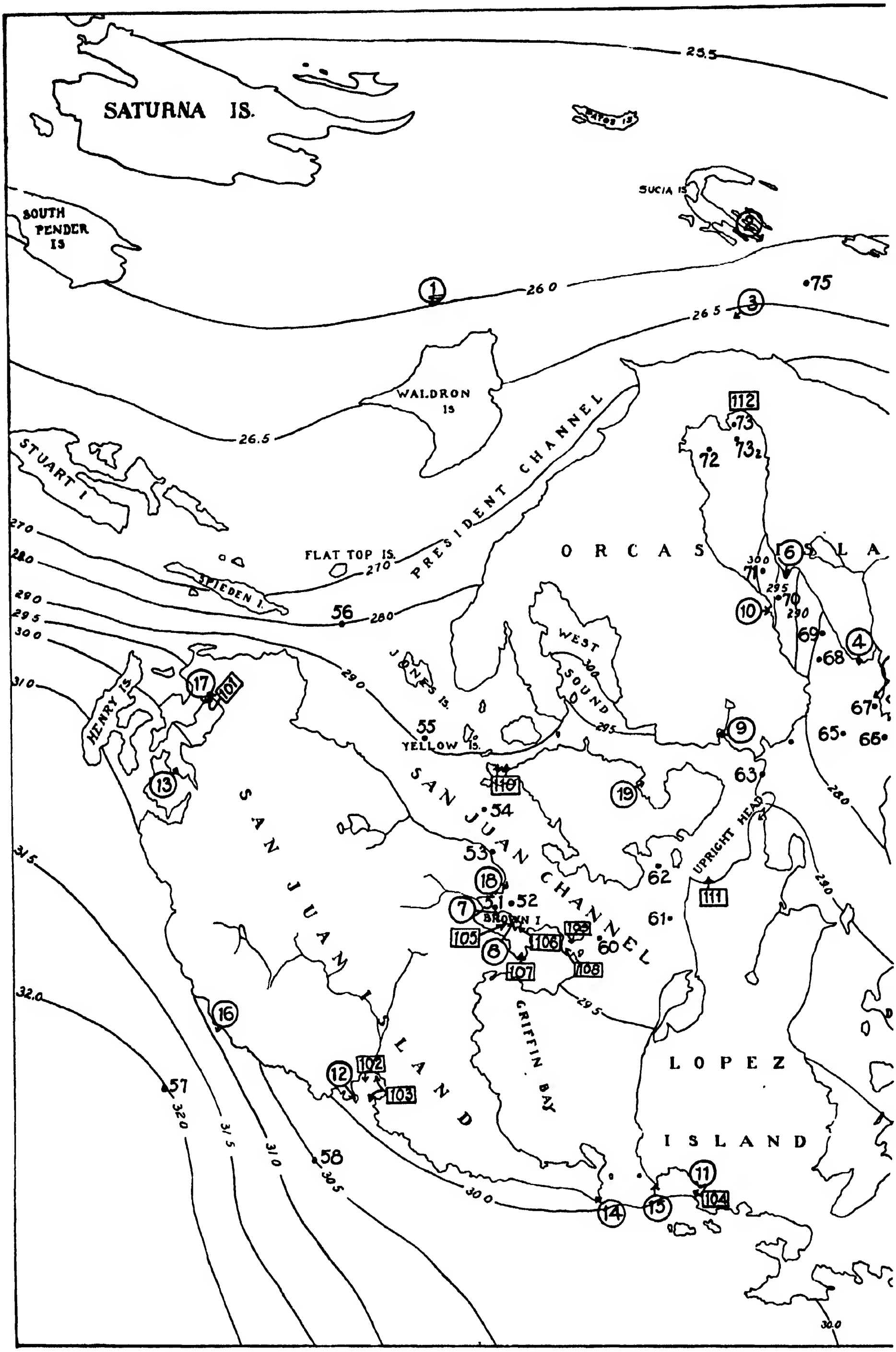

FIG. 1. Showing the estimated average relative summer salinity in grams of salts per liter, about the western half of the San Juan Islands and adjacent mainland and the location of stations. Dots = Dredging stations; Circles = Rocky shore stations; Rectangles = Sandy beach stations. The dot between 63 and 65 is station 64.

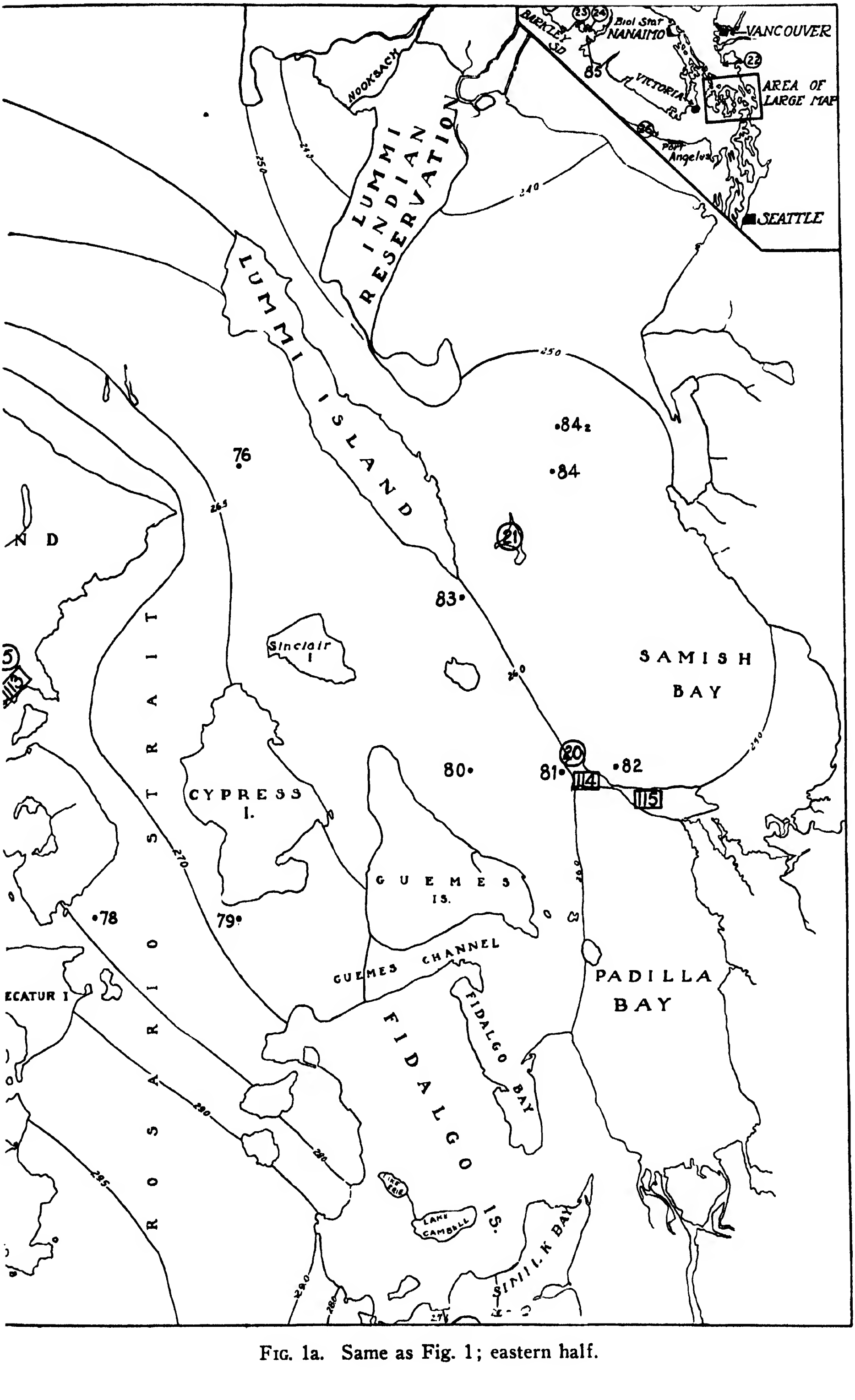

Fig. 1a. Same as Fig. 1; eastern half.

locations of the lines are based upon the shore communities and the proximity to rivers, as well as the published chemical work (Johnson and Thompson, '29; Powers, '20; Thompson, Lang and Anderson, '27; Thompson, Miller, Hitchings, Todd, '29).

A large series of determinations of alkalinity made in 1930 indicated that 80 or 90 parts per million is more nearly correct than 105 given by Shelford and Towler ('25). Powers and Logan ('25) and Powers and Hickman ('28) studied the carbon dioxide-carbonate relations of the sea water using a new method. The pH of the water is taken without contact with the air, then the water aerated with air, and a second reading taken. From these results it is possible to estimate the CO_2 pressure. Considerable work on light penetration into the water has been done since 1925. (Shelford and Gail, '22; Shelford, '29; and Williams, '29.)

2. METHODS

The Petersen bottom sampler was used almost exclusively, particularly in the studies of the communities in the waters about the southern portion of Orcas Island. A Sigsby trawl proved to be considerably more effective in securing fishes and other motile animals than the dredge.

A new quantitative net (Fig. 2) was used. It was designed by Dr. David H. Thompson of the Illinois Natural History Survey and proved to be very effective in securing small motile organisms. It was based upon the general principles of a casting net and was a cylindrical, conical topped net with numerous weights on the bottom ring. Modifications of the casting net consisted in providing an iron hoop to support the top of the net and a heavy central lead ring which tended to keep it on the bottom while the weights were being drawn together. See Fig. 2. The ring weight was released by a trip hook similar to that used on the Petersen bottom sampler. In Fig. 2 the net is shown in position for lowering. The net cylinder 4 ft. 6 in. high and 8 ft. in diameter hung from the hoop. The top was conical, the webbing reaching to the heavy weight ring. When the net was lowered into the water, the lead sinkers first rested on the bottom, then the hoop, finally the heavy ring. With the weight all released, the trip unhooked, leaving the weight ring resting on the bottom. When the rope to which the apparatus was attached was drawn up, the bottom of the cylinder net dragged over the sea floor to the central metal weight ring before the latter raised off the sea bottom. The bottom of the net was thus shirred together. While moving toward the center it dragged over the bottom and the animals resting there were forced to creep on top of it.

When it went straight down, this net covered 5 m^2 of bottom and in shirring together the bottom of the net dragged over less than 5m^2 as it often went down obliquely. The apparatus was therefore considered as covering

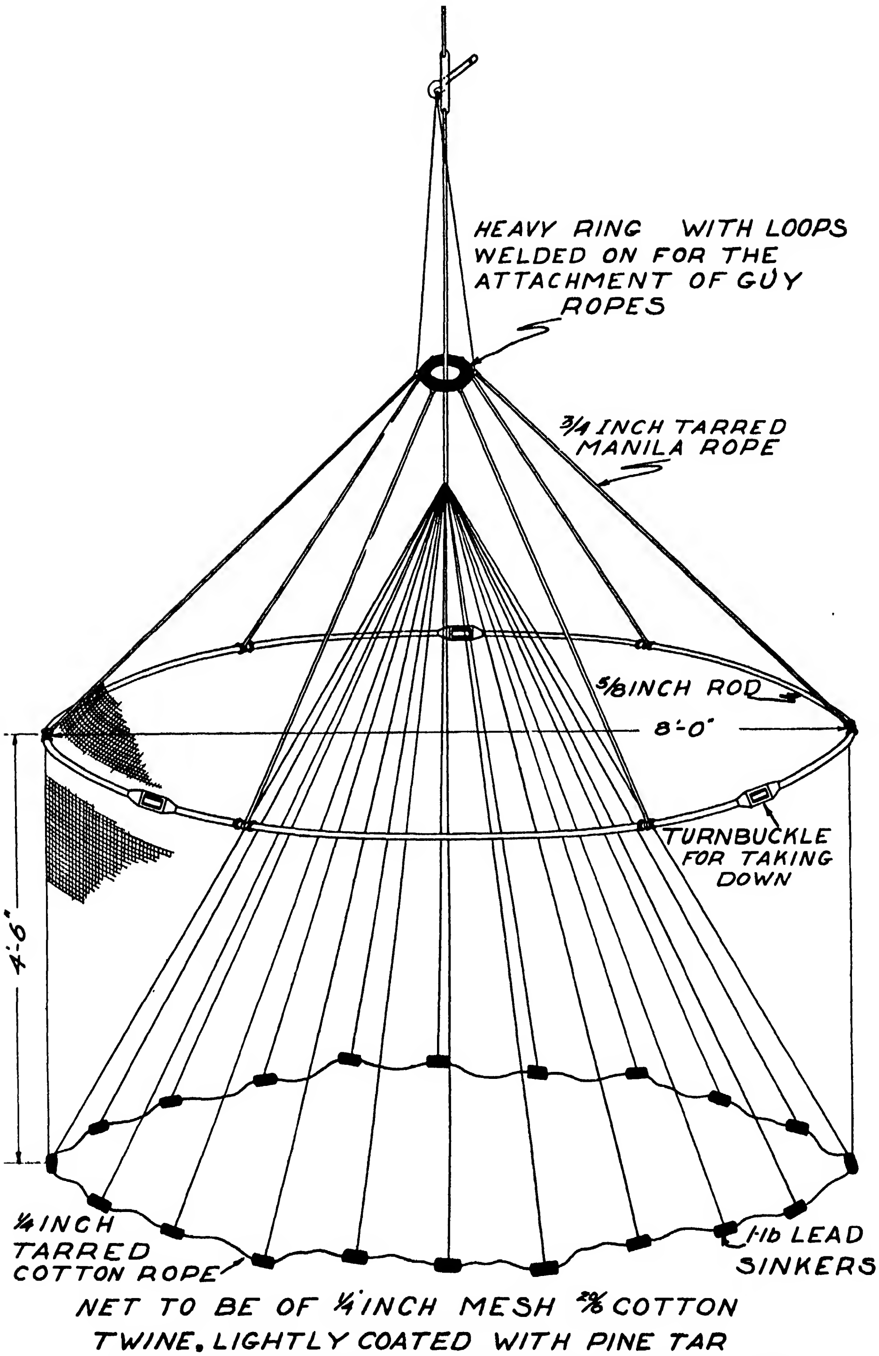

FIG. 2. Showing the closing net used for slow moving animals; for operation see text.

$4m^2$ of bottom. It was very effective in securing shrimps, crabs, and slow moving fishes. The difficulty with the net was the slowness with which it sank to the bottom and this difficulty was exaggerated by the necessity of using a very heavy cable attached to an awkward winch. In spite of these difficulties, however, it added very materially to knowledge of the communities studied. For the larger animals a net of much larger mesh and size would be necessary. The bottom rope must be very flexible or it could possibly be made of chain with small smooth links.

3. COMMUNITIES

The major communities[4] included in the area under consideration may be defined as follows:

III. Pelagic Communities

IV. Communities Associated with the Bottom (Figs. 3 and 4)

- A. Pandora-Yoldia Biome } Bivalve-annelid communities
- B. Macoma-Paphia Biome }
- C. Strongylocentrotus-Argobuccinum Biome } Gastropod-barnacle communities
- D. Balanus-Littorina Biome }

All but the Pandora-Yoldia biome were mentioned in the earlier paper (Shelford and Towler '25). The map (Fig. 3) indicates the more important bottom communities of the area and their subdivisions. Their arrangement in a cross section between Bellevue Point on the northern half of the west coast of San Juan Island and South Bellingham, Washington, on the mainland is shown in Fig. 4. The land area is omitted. One of the communities indicated is a faciation of one of the associations of the Strongylocentrotus-Argobuccinum biome. It occurs along the shore just below low tide practically throughout the Pandora-Yoldia area, except off clam beaches.

III. PELAGIC COMMUNITIES (MURRAY AND HJORT '12; GRAN '12 AND '31)

While none of the investigators concerned in this monograph have conducted intensive or quantitative investigations of this community, it is of such great importance in the modification of conditions surrounding other communities that a discussion of some of its features is essential. The pelagic community includes the plankton or floating organisms taken together with the swimming animals or nekton. The separation into those two groups as a basis for investigation has led to unfortunate failure to recognize the pelagic community proper. The density of population profoundly influences: (a) the penetration of light, (b) the food and chemical conditions in deeper water and at the bottom, and (c) the character of the bottom.

[4] A casual attempt (Shelford '16) with the advice of an algologist to use Forbes' Shore, Laminarian, and Coralline Zones which have no actual community basis was unfortunately copied in Pearse's Animal Ecology.

1. PLANKTON

It is not possible to agree with Allen ('21) and other algologists that diatoms of certain species are dominants or to refer to minute animals in similar terms. They do not take possession of the territory (*i.e.* volume) and hold it to the exclusion of other plants and animals. Their rôle is merely one of abundance of individuals and altogether weaker than is implied by "dominant." Diatoms, protozoa, etc., are the *vedomins*[5] of the pelagic community. Although selection may occur, the smaller planktonts are eaten by larger organisms with so little discrimination as to *species,* etc., that they serve a rôle similar to that of detritus and dissolved organic matter. The revival of interest in the latter has been stimulated recently by Krogh ('31).

Studies of the diatoms have been made by Gran *et al.* (Gran and Thompson, '30; Allen, '21-'29; Hutchinson, '28, '29; Cameron and Mounce, '22; Lucas and Hutchinson, '27; and Mounce, '22). Protozoa were studied by Eddy ('25); the Crustacea by Campbell ('29, '30), (also Lucas, '29; McMurrick, '16). Campbell ('29) found all types of smaller plankton organisms most abundant at a depth of about four meters. This included copepods, Peridinia, Tintinnidae, and diatoms.

On July 13, 1928, a series of eight water bottle samples were taken at depths of 1, 5, 10 and 20 m and 35, 50, 100 and 225 m at slack tide (station 56) over the Strongylocentrotus-Argobuccinum biome. Only twenty minutes intervened between the closing of the bottles in the two series. Counts of the diatoms by Dr. Gran showed that the maximum was at 20 meters. Diatoms were about 1/10 as abundant at the surface and 1/16 as abundant at 225 meters as at the maximum.

On the same date, over the Pandora-Yoldia biome (Fig. 1, station 69, see page 265), a series of four nearly simultaneous bottle collections (depths: —1, 5, 10, 20 m) in about 28 meters of water showed diatoms (counts by Dr. Gran) about 10 times as abundant as over the Strongylocentrotus community and the maximum was at 10 meters instead of 20 meters.

An examination of the animal plankton taken in nets hauled from the bottom to the surface within twenty minutes after each set of diatom collections just referred to, was made by J. C. Cross. The plankton over the Pandora-Yoldia community contained a few copepods, rotifers, and tintinnids, very many dinoflagellates, and various larval stages. That over the Strongylocentrotus-Argobuccinum community (see page 280) differed chiefly in the lack of dinoflagellates and in the presence of a greater variety of the larval stages. A few Sagittae were taken from the deep water here, but none over the Pandora-Yoldia community.

The only place where the larger animal plankton such as Crustacea,

[5] Professor Clements has proposed the use of *domin* for a weak type of dominance such as the larger pelagic animals exercise, and *vedomin,* meaning small domin, for the rôle of the minute planktonts.

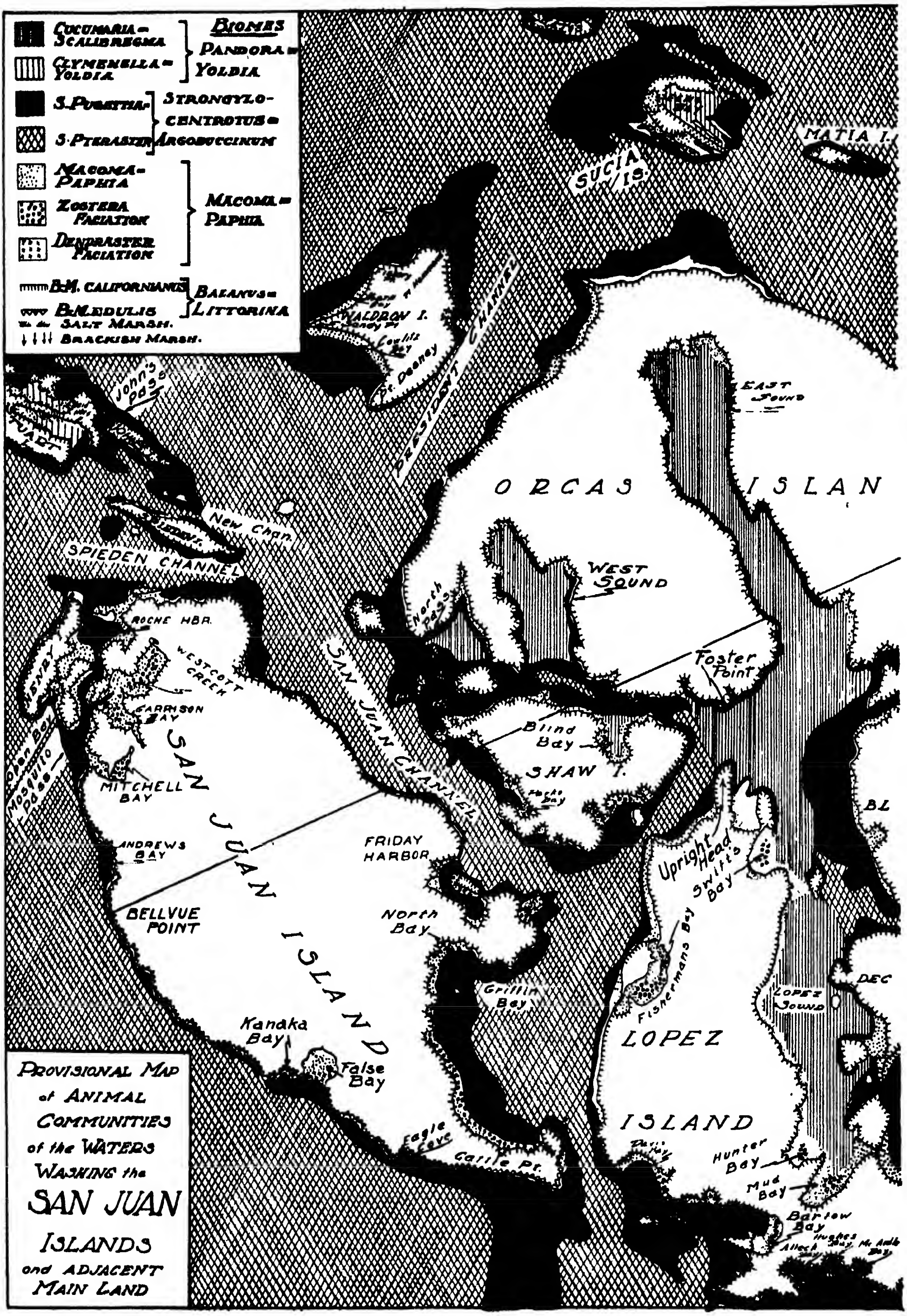

FIG. 3. Provisional map of the communities of the sea bottom about San Juan Islands. The associations and faciations are shown in the first column of the legend and the biotic formations or biomes in the last.

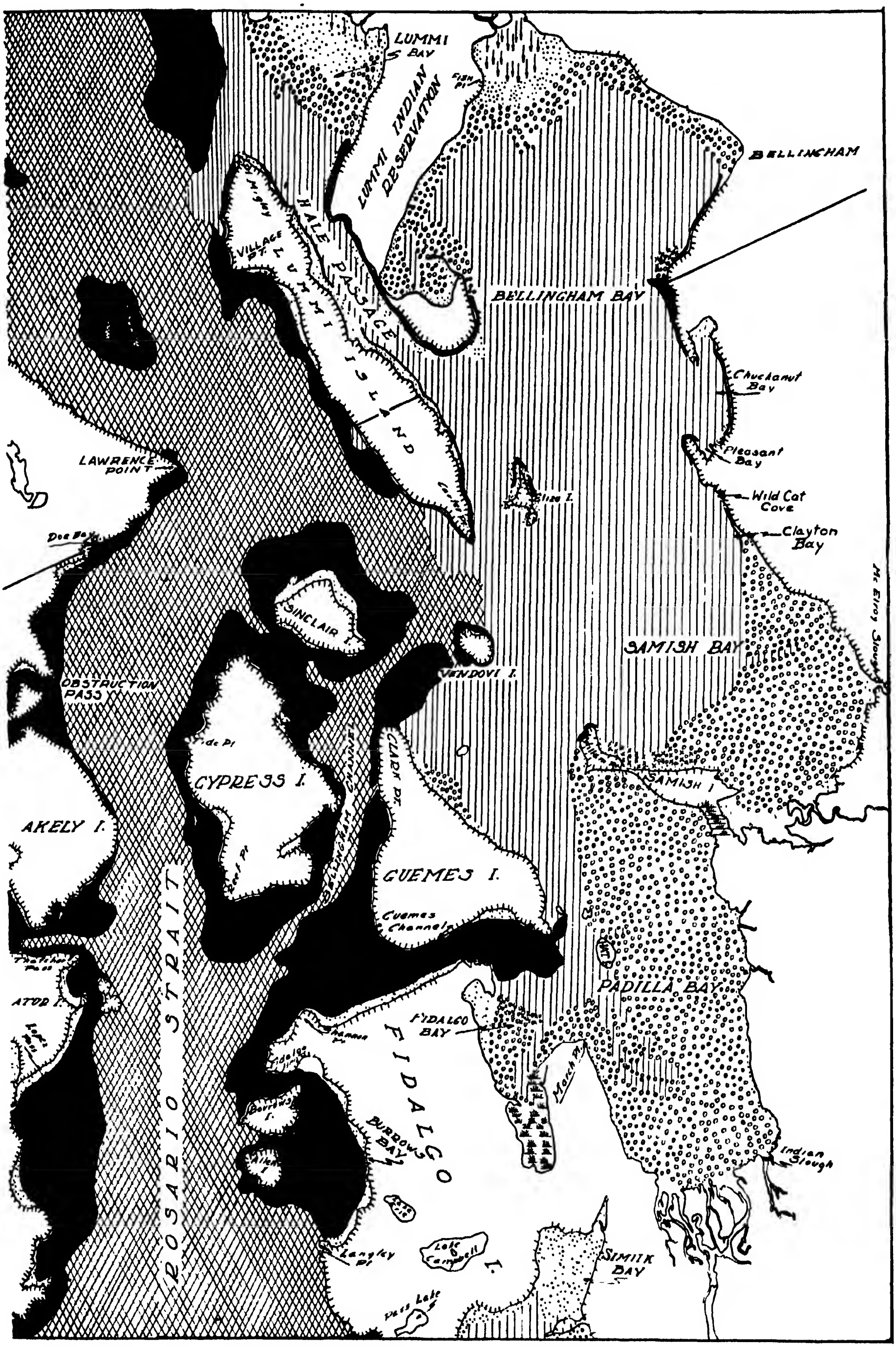

FIG. 3a. Same as Fig. 3; eastern half of the area.

Sagitta, etc., may be secured with certainty is on the south-west side of San Juan Island where salinity is highest (Fig. 1, station 57). These forms are either scarce or wanting or present only in deep water in San Juan Channel and waters nearer the mainland. This makes a distinct faciation in the waters near the mainland. Jellyfishes abundant during the summer months throughout both the inner and outer waters are: *Aequorea forskalea* P. and S., *Phialidium gregarium Haeck.* and *Thaumantias cellularia Haeck.* These together with less abundant species of Sarsia, Stomotoca, and Polyorchis and the common Ctenophores (Mnemiopsis and Pleurobrachia) make up a great part of the volume of the plankton of midsummer. There is a large seasonal element in the plankton, including many seasonal eggs and larval stages of various invertebrates and a few fishes (Bovard and Osterud, '18; Strong, '25).

2. NEKTON

The nekton or larger animals with effective swimming powers in this area consist largely of fishes and mammals.

(1) Pelagic Fishes (Kincaid, '19; Hubbs, '28)

The following have been taken more or less regularly and used in experimental work:

Clupea pallasii (Cuv. & Val.), herring (Shelford & Powers, '15; Shelford, '18; Powers, '21).

Hypomesus pretiosus (Girard), surf smelt (Shelford, '18).

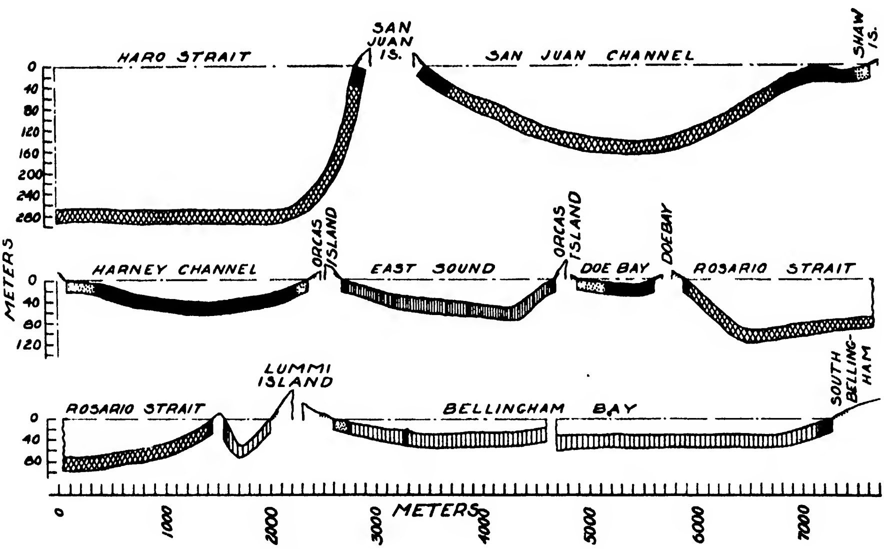

Fig. 4. Cross section of the Marine communities along a line passing through Bellevue Point on the west shore of San Juan Island and a point near the head of Bellingham Bay. The position of the line is indicated on Fig. 3-3a. The vertical scale is 5 times the horizontal; the legend is the same as in Fig. 3.

Thaleichthys pacificus (Richardson), eulachon.
Spirinchus starksi (Fisk), night surf smelt.
Allosmerus attenuatus (Lockington), white bait.
Oncorhynchus nerka (Walbaum), sockeye salmon; anadromous.
Oncorhynchus kisutch (Walbaum), silver salmon; anadromous (Powers, '21).
Oncorhynchus gorbuscha (Walbaum), hump-back salmon; anadromous (Shelford & Powers, '15).

(2) Pelagic Mammals

Orcinus rectipinna (Cope), killer whale.
Rhachianectes glaucus (Cope), gray whale.
Globicephala scammonii (Cope), Pacific blackfin.
Phocaena phocoena (Linnaeus), porpoise.

The killer (Orcinus) appears to be most abundant and was frequently seen in the San Juan Channel. In 1928 a school of killers came directly toward shore off Parker Reef, which rises abruptly from deeper water, at full speed until about 15 or 20 m off shore when they turned sharply to the left and avoided stranding. The blackfin was seen less frequently. The gray whales congregate in muddy bays and come to the surface daubed with bottom mud. In 1922 a light-colored whale (thought to be Rhachianectes) passed south between Brown Island and San Juan Island. Killers have been seen in the same location.

3. INTERACTIONS

Interactions are commonly divided into coactions or relations between organisms and reactions or effects upon the conditions of the habitat.

A. *Coactions* (Weaver and Clements, '29)

The coactions such as food relations are little known. The work of Lebour ('19 to '23) makes possible inferences as to the food of plankton animals and young fishes. The food of only a few adult fishes have been studied. The killer whale is known to feed upon fishes, salmon being mentioned especially (Scammon, '74), and also upon other whales. The same author states that the blackfish feeds upon squids and fishes.

B. *Reactions on the Habitat* (Clements, '05)

The plankton and other pelagic animals produce an important marine climatic reaction. They shut out much light from the waters below (Shelford and Gail, '22; Shelford, '29) and in sinking to the bottom at death consume much oxygen and produce carbon dioxide (Atkins, '22), sulphur compounds, and organic mud, having a profound effect upon bottom conditions, especially in quiet water.

4. PHYSIOLOGICAL CHARACTERS OF THE COMMUNITY

The independence of the bottom and shores is striking. Most of the work on physiological characters has been concerned with fishes. These are very sensitive to differences in the character of the water. Herring can recognize differences of 0.1°C. (Shelford and Powers, '14). These authors further showed that herring and salmon do not recognize differences in salinity but select their optimum hydrogen-ion concentration regardless of salinity. Powers ('21) confirmed this and followed the herring in its migrations in San Juan Channel. He found them closely associated with certain hydrogen-ion concentrations. Oxygen content and salinity appear to affect the reaction, however, and his findings as to exact pH do not hold good in other waters. Powers ('21) also studied juvenile salmon of two species with similar results. Rheotactic response of the sockeye is partially controlled by the oxygen content of the water (Daugherty and Altman, '25). Weese and Townsend ('21) showed that the jelly fish, Aequorea, moves downward when in contact with an adverse condition.

The resistance (Shelford, '18) of the herring and surf smelt *(Hypomesus pretiosus)* to CO_2 and other products resulting from adding small quantities of sulphuric acid (H_2SO_4) to the sea water was rated as 10 and 8 respectively while that of the viviparous perch, a shore vegetation inhabitant, had a resistance of 25. When sulphurous acid (H_2SO_3) was used in the same way the resistance of pelagic herring was rated 10; the viviparous perch from shore vegetation 21, and a bottom flounder 1100. H_2SO_3 may result from decomposition at the bottom. Other experiments by Shelford and Powers ('15) showed similar relations. We are justified in concluding that the pelagic fishes are much more affected by the condition of the water than shore and bottom species.

IV. COMMUNITIES ASSOCIATED WITH THE BOTTOM AND SHORE

These fall into two classes: (1) those dependent upon small water movements, much plankton, soft bottom of sand and mud (Pandora-Yoldia and Macoma-Paphia biomes) and (2) those on various relatively hard bottoms (Strongylocentrotus-Argobuccinum and Balanus-Littorina biomes) and much current or wave action. The first group is characterized by bivalve mollusks and annelids; the second by barnacles and gastropods. One of the latter, the Balanus-Littorina biome, has frequently been called inter-tidal, and the shoreward bivalve-annelid communities have been designated as "intertidal" also because a portion is exposed at low tides. This has led to much confusion and it is best to apply merely the term *tidal* to the Balanus-Littorina community and no other.

A. PANDORA-YOLDIA BIOME (A BIVALVE-ANNELID COMMUNITY)

In the discussion of the biome in general, mention is made of conditions and species which characterize the biome as a whole. Of necessity some of these are mentioned again in the discussion of its subdivisions. This biome approaches some of the communities described by Blegvad ('15-'30); Davis ('23-'25); Ford ('23); Hunt ('25); Jensen ('19); Petersen and Jensen ('11); and Petersen ('14-'18).

1. CONDITIONS

This community occurs on mud or soft bottom in 3 to 75 meters in Bellingham and Samish Bays, Padilla Bay, Lopez Sound, East Sound and much of the bay between Orcas Island on the north and Lopez and Blakely Islands on the south, including all of West Sound, North Passage, Deer Harbor, Echo Bay (in Sucia Island), and probably Reed Harbor and Hale Passage, though these have not been studied (Fig. 1, stations 63-73 and 80-84; Fig. 3).

The marine climatic conditions (Huntsman, '20) are quite different from those of other communities. The water is shallower, becomes warmer and produces many more diatoms. Tidal currents are weaker than in the San Juan Channel and the oxygen and salinity are usually or variably lower. The large amount of decomposition from the enormous production of diatoms is very great, yielding sulphur compounds and reducing the oxygen at the bottom. The small amount of oxygen could not be determined by the Winkler method in samples taken at the bottom because of the presence of sulphur compounds. Powers ('20) found the surface hydrogen ion concentration low as indicated by pH approximately 8.00. This is lower than over the Strongylocentrotus-Argobuccinum biome. The light is reduced greatly by diatoms. The usual scale of reduction down to 10 or 20 m. is crowded into 5 to 10 m. in this area (Shelford, '29, cf. Figs. 3 and 4a.). The community is best developed in areas of comparatively low salinity and high temperature with a large diatom population in summer. Attached algae are usually wanting or very few in number.

2. BIOME PREVALENTS OR PREDOMINANTS

A. *Dominants and Slow-Moving Influents*

Figures indicate the maximum and minimum of individuals per 10 m^2.

Pandora filosa Carp., asymmetrical bivalve; 20-350.

Yoldia limatula Say, yellow bivalve (Drew, '99); 1-541.

Marcia subdiaphana Carp., thin shelled clam; nearly always present, 1-90.

Sternaspis fossor Stimp., gooseberry worm; 10-460.

Amphicteis alaskensis Moore, worm; 1-100.

Phacoides tenuisculptus Carp., snail; 0-400.

Luidia foliolata Grube, starfish; common to abundant, 1-10.

Pycnopodia helianthoides (Brandt), 20 rayed star; 1-3.

B. *Influents*

Crago alaskensis (Lock.), shrimp; usually present, 1-20.
Lyconectes aleutensis Gilbert, red devil; common.
Crabs are few and not important. Hermit crabs are especially few.[6]

C. *Characteristic Species*

Cerebratulus montgomeryi Coe, large nemertean.
Dentalium rectius Carp., tooth shell.
Yoldia thraciaeformis Storer, large Yoldia.

These species are distributed throughout the biome and constitute the binding dominants and influents. The biome is divisible, however, into two or possibly three associations which include these dominants and along with them others of restricted range. The associations recognized are the Cucumaria-Scalibregma association, the Clymenella-Yoldia association and the Diopatra-Chelyosoma community, which covers a very small area and is here considered as representing an ecotone rather than a distinct association. This status is provisional and may be changed when other examples have been discovered and studied.

3. ASSOCIATIONS

A. *Cucumaria-Scalibregma Association*

(1) Conditions.

The bottom consists of mud composed of fine silt, much of which is quartz, mixed with organic detritus, especially diatom detritus in various stages of decomposition (Jensen, '14). An examination of the bottom sediment in East Sound was made on August 7, 1928, about one kilometer into the Sound. The fresh part of this sediment was 5 cm. deep, down to the darker mud of the year before. The upper part consisted of plankton detritus, other plant and animal material and a small amount of fine transparent sand with grains of various shapes and sizes. The amount of this sand increased in the deeper parts but organic detritus still equaled or exceeded the sand in volume. These fine quartz particles were nearly always in evidence under the microscope in the plankton collections secured with a tow net from San Juan Channel. The principal sources of this material are the Fraser and Nooksack rivers. The character of the bottom is similar throughout, though the amount of organic material appears to increase toward the upper end of East Sound (Weese, page 310).

It has already been noted that the oxygen content of the Puget Sound water is always about 1 cc. per 1 below saturation for pure sea water. The oxygen at the sea bottom in these waters is generally very low and the iodine

[6] *Nucula castrensis* Hinds, camp nut shell, is local and usually on the border of the community where it meets the Strongylocentrotus-Argobuccinum community; also in mud pockets in the S. A. community.

absorption of samples so great that the small amount of iodine liberated by the Winkler method is quickly, if not immediately, absorbed, rendering its determination unusually difficult. The oxygen content usually decreases from the surface toward the bottom. The carbon dioxide content is doubtless high and other products of decomposition such as hydrogen sulphide, etc., are very important.

The diatom plankton of this area is frequently extremely dense (Gran and Thompson, '30) especially in East Sound. The enormous phytoplankton production about the mouth of the Fraser River appears to supply some diatoms (Lucas and Hutchinson, '27) which appear to drift in from the Rosario Strait. Many are produced locally under the stimulus of high temperature. Their density is so great as to transmit only 2% of the violet, blue, green, and yellow light (average of the four colors) to 8 m, while in the clearer water of the San Juan Channel, 13% is transmitted to 8 m. This phytoplankton has a pronounced effect upon the conditions at the bottom not merely in producing deritus but in modifying light (Shelford, '29) with a very marked effect upon the character and success of the life at and just above the bottom.

(2) Dominants and slow-moving Influents.

The expanding worm (Scalibregma) is very important and has increased in importance during the period in which the community has been observed. It occurs in the Danish waters and is a pure detritus eater (Blegvad, '14, p. 60). The white cucumber, *Cucumaria populifera* (Stimp.), is very abundant also and is probably a pure detritus eater; as is also the larger spotted cucumber, *Cucumaria piperata* (Stimp.), which is confined to the shallower water. The biome prevalents listed on page 265 occur mixed with the species characteristic of the association. Figures indicate the maximum and minimum number of individuals per 10 m^2.

Scalibregma inflatum Rathke, expanding worm; 1-9600.
Cucumaria populifera (Stimp.) Theel, white cucumber; 1000-8000.
Luidia foliolata Grube, fragile starfish; 1-10.
Pycnopodia helianthoides Brandt, 20 rayed starfish; ½-1.
Yoldia limatula Say, yellow bivalve; a detritus eater (Drew, '99); 10-500.
Pandora filosa Carp., asymmetrical bivalve, a detritus eater; 10-300.
Ophiopholis aculeata var. *kennerlyi* (Lyman), brittle star; usually present.
Amphiodia occidentalis (Lyman), brittle star; abundant 1926.

(3) Influents.

Crago dalli (Rath.) shrimp; 1-48, 1926.
Neomysis kadiakensis Ort., shrimp; abundant in 1930 circular net catches.
Lycodes brevipes Bean, short finned eel-pout; present 1926, 1928, 1930.

Lycodopsis pacificus (Coll.), Pacific eel-pout; present 1926, 1928, 1930.
Psettichthys melanostictus Gir., black spotted flounder; present 1926, 1928.
Porichthys notatus Gir., midshipman; 1926, 1928.

(4) Characteristic species.

Serripes groenlandicus Beck., brilliant bivalve, very few.
Corolla spectabilis Dall., sea angel; few.

The existing knowledge concerning the interactions and other dynamic features of Pandora-Yoldia biome is based on this association. However, this is discussed in general terms on page 271 following the description of the association and the noteworthy variations within them. These have been termed faciations.

(5) Faciations.

In the area occupied by the association in typical composition, are included much of Deer Harbor, West Sound, Olga Bay, the outer third of East Sound and probably Lopez Sound. Throughout this area in water from three to six meters around the shore, there is a faciation characterized by *Cucumaria piperata* (Stimp.) which largely takes the place of *Cucumaria populifera* (Stimp.) and is frequently accompanied by tunicates. This may be designated as the Scalibregma-C. piperata faciation. The three other faciations of this association are described by Weese (page 310). These occur in the inner part of East Sound and presumably exist in West Sound and elsewhere. Those studied occur in waters more saline than those of San Juan Channel. They are in part due to the loss of prevalent species and in part due to the addition of other species of importance.

B. *Clymenella-Yoldia Association*

This association was not investigated with the bottom sampler, but merely by reconnaissance dredging. Only a few general points can be brought out regarding the bottom and other conditions. It is found in Bellingham and Samish Bays and adjacent waters.

(1) Conditions.

The bottom is soft oozy mud, and contains more terrigenous matter than the bottom associated with the Cucumaria-Scalibregma association, and has a slightly yellowish color. The difference in taxonomic composition of this association as compared with the preceding one is very striking, principally on account of the very large number of worms of the genus Clymenella. The biome prevalents listed on page 256 occur mixed with those listed below.

(2) Dominants and slow-moving Influents.

Clymenella rubrocincta John., bamboo worm; very abundant.
Dendronotus giganteus O'Don. giant nudibranch; abundant.

Yoldia ensifera Dall, yoldia; common.
Scalibregma inflatum Rathke, expanding worm; few.
Glycera sp., worm; few.
Nucula linki Dall, bivalve; common.
Glycinde armigera Moore, annelid.
Pandora filosa Carp., asymmetrical bivalve; present.
Luidia foliolata Grube, fragile starfish; common.
Amphitrite robusta John., terebellid worm.
Crago franciscorum (Stimp.), Frisco shrimp; common.
Polinices groenlandica (Beck) Möll., moon snail.
Amphiodia urtica (Lyman), brittle star.

(3) Influents.

This class appears few both in species and number, in part due to our failure to investigate the fishes.

Crago alaskensis (Lock.), shrimp.
Crago communis (Rathbun), shrimp.
Hyas lyratus Dana, crab; few.

The *faciations* of this community have not been studied. No experimental work has been conducted on its characteristic animals.

4. EXTENT, RANK AND BOUNDARIES

The extent of this biome is quite unknown but the boundaries of the portion studied are sharp and ecotones are narrow. The definite habitat (hydrographic) conditions which it requires, are to be found in numerous inlets along the Pacific coast of North America. The distribution of the dominants and slow moving influents as given in economic and taxonomic literature indicates a considerable range both into Alaskan and into Southern Californian waters. This literature is an unreliable and even a treacherous guide, but usually species are important community constituents over half at least their range.[7] It seems best to consider the small area studied as a disconnected portion of a much fragmented biome, probably widely distributed in protected inlets.

A. *Ecotone Communities*

Diopatra-Chelysoma ecotone between Pandora-Yoldia and Strongylocentrotus-Argobuccinum biomes. This occurs between Upright Head and Foster Point, in the eastern portion of Harney Channel in depths of 50 to 75 m.

The bottom is of soft mud, but somewhat denser than in the shallower bottoms, due to the terrigenous materials from adjacent rivers. There is

[7] There are many examples of the failure of such distribution records. In primeval times the white pine, for example, occurred in scattered, insignificant patches and as single trees over twice as much territory as it occurred as a general dominant.

much less plankton detritus and fresh organic matter. The circulation at the bottom presumably is greater than in the other situations.

This community covers such a small area that while it is fairly distinct it is best to leave the determination of its status until such a time as further examples have been found. Since the character is in part a matter of depth, there is little bottom in the region of study which could be expected to have this type of community. While a considerable number of forms occur, which *belong properly to the Strongylocentrotus*-Argobuccinum biome, notably *Pecten hericius* Gould and the crabs, Cancer and Oregonia, it lacks several characteristic species found on similar bottoms in the Strongylocentrotus-Argobuccinum areas. *Modiolus modiolus* Linné is essentially wanting here. Green sea urchins rarely occur. Some of the fishes of the Strongylocentrotus area are occasionally present.

(1) The following are the chief dominants and slow moving Influents.

Figures indicate the maximum and minimum number of individuals per 10 m^2.

Diopatra californica Moore, ornamented tube worm; 125-200.
Chelyosoma productum (Stim.), flat topped tunicate; 5-100.
Marcia subdiaphana Carp., thin shelled bivalve; 10-150.
Styela gibbsii (Stim.), tunicate; 1-20.
Large sea anemones, a few always taken.
Pectinaria brevicoma John., sand tube worm; 1-30.
Pycnopodia helianthoides (Brandt), 20 rayed star; 1-2.
Nucula castrensis Hinds, truncated bivalve; 1-40.
Phyllochaetopterus sp., bamboo tube secretor; 20-60.
Ophiura sarsii Lütk., brittle star; usually present.
Pecten islandicus Muell., scallop; 2-8.

(2) Influents.

Ronquilus jordani (Gilbert), Jordan's ronquil; present 1928.
Porichthys notatus (Girard), midshipman; 1928.
Lycodopsis pacificus (Coll.), Pacific eel-pout; 1930.

(3) Characteristic Species.

Cardium ciliatum Fabr., small cockle.

B. *Shallow Water Ecotone Communities*

The shallow water ecotone community lying between the Pandora-Yoldia biome and the Strongylocentrotus-Argobuccinum biome is characterized by various tunicates. These are *Chelyosoma productum* (Stim.), the flat top tunicate, *Styela gibbsii* (Stim.), and *Pyura haustor* (Stim.). Large red sea anemones are common as in the deeper water ecotone. *Trichotropis cancellata* Hinds occurs among the Pandora-Yoldia species.

Where the shore is sandy there is an ecotone between the Pandora-Yoldia

biome and the Macoma-Paphia biome, characterized by the presence of Paphia, *Macoma inquinata* Deshayes, hermit crabs, flat fishes, etc.

5. INTERACTIONS

The worms, sea cucumbers, and bivalve mollusca probably feed heavily on the detritus at the bottom while the starfishes feed upon the bivalves and cucumbers. The large size and considerable numbers of the starfishes should make them potent influents upon the more stationary members of the community. Fishes probably take as heavy toll of the sedentary types as do the starfishes (Stevens, '30).

The reaction of the pelagic community, on the bottom is very marked as regards lights, etc., and has been pointed out. The numerous burrowing worms and mollusks tend to bury and consolidate the organic matter with the terrigenous deposits (Moore, '31).

6. ANNUATION

There were many variations in numbers of individuals per unit area and in species present between 1926 and 1930. Table 1 shows these relations.

TABLE 1. Showing the variation in numbers of several invertebrates per 10 m^2 in the Pandora-Yoldia biome. X indicates presence in very small numbers. The location of stations is shown on Fig. 1, page 254.

Species	Station	1926	1928	1930
Yoldia limatula Say and *Yoldia ensifera* Dall	63	200	360	25
	64	541	200	10
	67	X	X	16
Pandora filosa Carp.	63	X	X	X
	64	350	100	120
	67	40	30	20
Marcia subdiaphana Carp.	63	90	70	13
	64	16	15	0
	67	20	30	20
Scalibregma inflatum Rathke	63	0	X	300
	64	0	X	320
	67	950	X	1820
	68	X	1350	9610

7. LIFE HISTORIES AND PHYSIOLOGICAL CHARACTERS

The Mollusca of this community have apparently not been studied locally. In a similar community in the Danish waters (Jensen '19), studied growth rings showing periods of growth in important Mollusca covering from two to nine years. Blegvad ('28) indicates that some of the Mollusca of the Danish community (e.g. *Abra alba*) do not live beyond the second summer. The life histories of the animals without hard skeletons are not known. Little

physiological work has been done. The black spotted flounder which is found in this community was found by the writer (1918) to be a hundred times as resistant to H_2SO_3 and fifteen times as resistant to CO_2 as the herring. This is in keeping with its ability to live on decomposition-laden bottoms.

8. COMPARISON WITH DANISH COMMUNITIES

The activities, reactions, and food habits of the animals of this biome have not been studied. The same is true of physiological responses; this was due chiefly to the distance from the biological station. Blegvad ('14) made extensive studies of similar communities in Danish waters, including studies of the food habits of a few of the Pacific species. None of these have comparable significance in both the Danish and Puget Sound waters but the comparisons suggested in Table 2 and 3 are important.

TABLE 2. Species common to the Danish and Puget Sound Waters (Blegvad, '14, '16).

	Abundance		Blegvad's Classification as to food habit
	Danish	Puget Sound	
Scalibregma inflatum Rath...........	Relatively few	Very abundant	Detritus eater
Ophophiolis aculeata (Linn.) Gray.....	Abundant	Few	Carnivorous detritus eater

TABLE 3. The following species belong to the same genera as those discussed for the Danish waters and probably have similar habits (Blegvad, '14, '16).

Puget Sound species	Food habits of species of the same genus in the Danish waters
Dendronotus giganteus O'Don........................	Carnivorous detritus eater
Glycera sp..	Carnivore
Nephthys coeca Fabr..................................	Carnivore
Lubrinereis bicirratus Tread.........................	Carnivore
Dentalium rectius Carp...............................	Carnivorous detritus eater
Macoma expansa Carp.................................	Detritus eater
Polinices groenlandica (Beck) Moll...................	Purely carnivorous
Nucula linki Dall......................................	Detritus eater
Styela gibsii (Stimp.).................................	Detritus eater
Marcia subdiaphana Carp..............................	Detritus eater
Cucumaria populifera (Stimp.)........................	Detritus eater
Cucumaria piperata (Stimp.)..........................	Detritus eater
Crago alaskensis (Lock.).............................	Carnivorous detritus eater
Crago communis (Rathb.).............................	Carnivorous detritus eater

B. MACOMA-PAPHIA BIOME (AN ANNELID-WORM COMMUNITY)

1. LIFE FORMS AND CONDITIONS

The life forms of this community resemble those of the Pandora-Yoldia biome. Bivalves and worms are important and starfishes and flatfishes occur. The native bivalves of the Macoma community usually are not abundant

beyond about 1m *above* mean low tide and usually are very scarce above 1½m. However, this distribution is greatly modified by the water-holding capacity of the soil or bottom materials. The habitat is covered with sea water at its upper edge about 60 per cent of the time (Shelford and Towler, '25, page 46) and the beach materials usually hold water in quantity while the tide is out.

In the work of Shelford and Towler ('25) this community was not investigated or understood below low tide line. Petersen has pointed out that *Macoma balthica* Linn. and *Mya arenaria* Linn. (the latter introduced in the Pacific) are important dominants in the similar biome in the Baltic and the coastal waters of northern Europe and extend down to 20 or 30 m. in a few places. He believes that this community is restricted to shallow water because of the destruction of young stages by echinoderms.

The climate of this community varies from that of the Strongylocentrotus-Argobuccinum biome in quiet bays to that of the Pandora-Yoldia biome. The influence of the substratum here is of greatest significance in shallow water and is concerned with its water holding capacity while the tide is withdrawn. Bruce ('28) has made a study of this property of beach sands. The community is highest up on the beaches with finest sand of greatest water holding capacity. A comparable community disappears quite completely above the low water mark on open shores of the Pacific. Fraser and Smith ('28) state that "the position in relation to tidal currents and exposure or protection from storms has much more to do with the rate of growth of clams than the actual composition of the beach." Smith ('28) found growth correlated with quantity of plankton.

The dominant clams find optimum conditions, as indicated by abundance at different levels, between one and ten meters below high tide. The maxima differ in position for the different species, on different shores and beaches and in different years. In some years there is a definite order among the species; in others considerable irregularity occurs. Quite frequently maxima occur at two or more levels, often explainable on the basis of water holding capacity of the sand. Not infrequently *Macoma nasuta* and *M. secta* are at a maximum at about the mean of the lowest 6 or 8 tides of each month.

Wismer and Swanson (p. 340) found more of the clams at about 9 or 10m than at 3m below high tide. Most of the dominants are found at a depth of 10m. *Cardium corbis* occurs at the lower limit of the community. Paphia staminea is distributed to a considerable depth, perhaps as much as 100m in very small numbers. It is alleged to show shell modifications which distinguish deep and shallow water individuals. The greatest area of the community and the greatest total number of individuals is subtidal; the remainder are bathed in the waters held by the beach during low tide. The community is essentially subtidal.

The introduced *Mya arenaria* ordinarily is found higher on beaches than any of the native species, and *Macoma nasuta* and *Macoma balthica* are found highest of the common native species. *Tellina carpenteri* Dall which occurs in only a few places is found as high as Mya. Crabs of the family Pinnotheridae are common in clams and in Upogebia holes.

2. BIOME PREVALENTS OR PREDOMINANTS

A. *Dominants and Slow-Moving Influents*

The figures indicate the maximum and minimum number of individuals per $10m^2$ at the point of maximum abundance on the beach. Those showing 0 are sometimes wanting on a particular beach.

Macoma nasuta Con., bent-nosed clam; 5-250.
Macoma secta Con., clam; 10-150.
Macoma inquinata Desh., clam; 20-250.
Paphia staminea Con., little-neck clam; 0-200.
Macoma balthica Lin., pink clam; 0-500.
Saxidomus giganteus Desh., clam; 0-30.
Cardium corbis Mart., cockle; 1-10.
Schizothaerus nuttallii, Con., giant clam, Washington clam or horse clam; local.
Nereis virens Sars., and other nereid worms; 4-140.

B. *Influents*

(1) With preference for open sandy areas.
Lepidopsetta bilineata (Ayres), sole.
Oligocottus maculosis Gir., tide pool sculpin; very common.
Psettichthys melanostictus Gir., black spotted flounder.
Platichthys stellatus rugosus Gir., starry flounder.
Liparis fucensis Gir., rock sucker.
Hemigrapsus oregonensis (Dana), hairy shore crab.

(2) With preference for eel grass (Zostera).
Cancer productus Rand., edible crab; common.
Cancer magister Dana, edible crab; common.
Telmessus cheiragonus (Tilesius), helmet crab; common.
Sebastodes maliger J. & G., rock fish.
Sebastodes caurinus (Richardson), yellow spotted rock-fish.
Sebastodes melanops (Gir.), rock fish.
Pholis ornatus (Gir.), green or chameleon blenny.
Pholis laetus (Cope), green or chameleon blenny.
Syngnathus griseolineatus Ayres, pipe fish.
Lumpenus anguillaris (Pallas), snake blenny.
Gasterosteus aculeatus aculeatus Lin., Alaska stickleback.

Pagurus granosimanus (Stimp.), hermit crab; see Wismer and Swanson, p. 342.

Pagurus beringanus (Bened.), hermit crab; see Wismer and Swanson, p. 342.

Pallasina aix Starks., Pallas' sea poacher.

Ophiodon elongatus Gir., ling cod., juvenile.

3. ASSOCIATIONS

The study of this community has not been adequate for the detailed mapping and interpretation of the associations. In the work of 1922 and 1924 (Shelford and Towler, '25) two associations were recognized. These are, however, to be regarded as purely provisional.

A. *The Macoma-Paphia Association*

In addition to the prevalents listed on page 274 this association is characterized by the bivalves of these genera with Saxidomus and Schizothaerus and abundant nereid worms; it is in the more protected waters. There is no doubt but that a community of this composition quite generally occupies the smaller beaches among the San Juan Islands. Succession with physiographic change due to cliff erosion has been discussed by Wilson ('26).

B. *The Macoma-Leptosynapta Association*

This association occurs on the more exposed shores and evidently on the wide flat areas with Zostera such as False Bay and possibly some of the flats north of Samish Island and near Anacortes. Schizothaerus and Saxidomus are often wanting and *Paphia staminea* is far from abundant, while *Cardium corbis* is usually more prominent than in the other association. *Arenicola claperedii* Lev., smooth clam worm and *Tellina carpenteri* Dall, bivalve, and *Leptosynapta inhaerens* are characteristic of the community at False Bay (stations 102 and 103).

A reconnaissance on both sides of Samish Island (stations 114 and 115) where Zostera is abundant showed the usual assemblage of animals. *Cardium corbis* was conspicuous. *Saxidomus giganteus* was present and *Macoma nasuta* was fairly abundant but decreased with depth of water. A few *Paphia staminea* were found and young fishes were observed in the more open spaces among the eel grass. Sand dollars, *Dendraster excentricus* Esch. occur in two places (near mainland; records by Prof. T. Kincaid) and the conditions appear similar to the smaller area in False Bay. The coast north of Anacortes appears to resemble the great beds of Zostera described by the workers of the Danish Biological Station (Petersen, '11; Blegvad, '14). The detritus from these is of the utmost importance as the food of invertebrates which serve as food to the fishes. Because of the presence of sand dollars

which characterize a faciation these areas are suggested as in part at least of a composition similar to that of False Bay which has been provisionally designated Macoma-Leptosynapta association.

4. FACIATIONS

A. *Ulva Faciations*

The Ulva "association" of Muenscher ('15) lies in shallow water, frequently at least on the shoreward side of the Zostera. Ulva grows on the beach up to a point which is somewhat above mean low water, though its upper limit appears to vary from year to year. It often covers beaches more or less completely and increases their water holding capacity while the tide is out. Some of the plants appear to be detached and fragments of plants are common. It is often an important factor on beaches. It does not suppress the animal dominants common on the open sand areas which the Macoma-Paphia biome occupies.

In the quieter small bays and recesses of the shore, Ulva and a few other algae commonly grow among the eel grass. Here, however, only occasionally does it become a codominant associated with eel grass (*Zostera marina* Linn, and other species); (Muenscher, '15).

B. *Zostera Faciations*

Zostera marina L., eel grass, occurs in both the provisionally suggested associations, Macoma-Paphia and Macoma-Leptosynapta, but limited investigation renders detailed discussion impracticable. Eel grass is not uniformly distributed in either association. There are many local areas of eel grass but the large areas are near the mainland. These lies northeast of Samish and northeast of Fidalgo Islands and contain about 65 km^2 (26 sq. mi.). Zostera introduces an additional layer into the community by supporting several attached algae, especially Porphyra and sometimes Ulva and Enteromorpha, and the filamentous diatoms. These epiphytic plants increase the surface and hiding places so that the Zostera area supports more animals than it would otherwise. *Lacuna porrecta* Carp. is usually present; large amphipods unidentified; *Caprella* sp.; *Pentidotea resecata* (Stimp.), isopod; *Epiactis prolifera* Ver., sea anemone; and *Haminoea vesicula* (Gld.) occur, often in abundance (station 102). Lacuna does not occur on eel grass at a distance from rocks and kelp. The nearer these are the greater Lacuna's abundance. The same is true of the isopods. The sea anemone and the Haminoea are most abundant on muddy bottoms where there is evidence of succession toward land (near station 107). Sometimes there are many shrimps and crabs in the eel grass and at other times few or none are found. Young fishes are also sometimes abundant. All the motile forms appear to move in and out of the vegetation. European workers have shown that this

faciation is a very important feeding area for young cod, eel, plaice dab, flounder, etc. These relations have not been worked out for Puget Sound but eel grass areas may well be of great value to fisheries.

c. *Dendraster Faciations*

The sand dollar, *Dendraster excentricus* Esch., is abundant locally among the eel grass and is the only one of a series of characteristic forms in False Bay (station 103) known to be found locally in the large areas of eel grass of the flats near Fidalgo and Samish islands.

This striking addition to the usual community composition may entitle these areas to be ranked as sand dollar faciations though their local character may make them more properly termed lociations.

The Macoma-Paphia biome undoubtedly represents an important climax though much study of its development (succession) on new areas as well as much geographical and annual study would be necessary to interpret the series of associations, faciations, etc., included in the community.

5. EXTENT, RANK, AND BOUNDARIES

This community occurs in fragments in the areas of study and in general is characteristic of protected bays just as is the *Macoma (balthica)*-Mya community of Europe. The fragments of the biome taken together would cover a considerable area though its depth is slight. No evidence has yet been found for the community's extension to depths beyond the 8-10m below low tide. The range of bottom materials which it inhabits is great, including organic muck, finest silt, sand and fine gravel. The community is evidently wanting on open shores and bays facing the Pacific Ocean (Edmonson, '20).

6. INTERACTIONS

A. *Coactions*

Blegvad ('16) worked on the coactions in the Macoma-Mya community of the western European waters. He found that the bivalves of the portion of this community toward shore from the Zostera faciation were not eaten by fishes and thus grew to great size. This corresponds to the area from which clams are commonly dug on the shores of northern Oregon, Washington, and British Columbia. In the plant belt Blegvad found that the fishes feed on juvenile bivalves. There are also many food, shelter, and attachment coactions between the Zostera, the attached algae, and attached animals; also between the attached animals and the small and juvenile fishes which frequent the plants. Outside the Zostera faciation in the Danish waters where the bottom materials are finer the large food fishes devour the various bivalves and worms. The same is probably true about the San Juan Islands; the deeper water yields small specimens of the dominant bivalves. In our

area the flatfishes are sometimes on the shoreward side of the Zostera at high tide and may take food from the area; especially the young flatfishes are common here and may take juvenile bivalves. This subject should be studied in the interest of fisheries.

B. *Reactions*

All the community constituents react on the habitat but wherever it grows, Zostera is most important. It checks currents and wave action, produces shade and tends to hold the bottom materials. Fishes, bivalves and gasteropods move the bottom materials at the surface and the worms pass quantities of soil through their alimentary tracts. Upogebia is said to have completed the ruin of over-fished Pacific oyster beds. The native oyster bed is evidently a climax community (Stevens, '26, p. 348).

7. COMMUNITY DEVELOPMENT

Opportunity to study succession on new deposits not accompanied by low salinity, as about the mouths of rivers, are rare. One case not fully taken advantage of, near Friday Harbor, was studied enough to show that the investigation of quasinatural areas must be supplemented by actual experimental operations. The gravel deposit in the moraine which forms the south end of San Juan Island was utilized commercially on a large scale for two or three years ending in December, 1928. The gravel was run down a chute and over sorting screens into barges. This gave a large residue of the finer material which found its way onto the adjacent bottom. This deposition of quantities of silt reached a depth of 30 cm. or more at 500 feet from the barge loading point within a short time. The material from the line of chutes and screens produced a long peninsula which formed a small bay deeply silted with fine material which came from the gravel.

No examination of the community was made at the time operation stopped. Twenty months after the operation of the pit ceased, S. W. Howe made a careful census of animals of the area. The silt originating from the gravel was 50 cm. deep as a result of two or three years operation. Worms were plentiful. *Macoma nasuta, M. inquinata, M. identata, Paphia staminea,* and *Cardium corbis* were found. Total clams ranged from 10 to 84 per m^2. The life history of *Paphia staminea* has been worked out by Fraser and Smith ('28). This clam spawns in summer and thus the 1929 clams should be only a year old and about two-fifths of an inch long. Since the clams were much larger than this it became evident that they had survived the rapid silting and that some additional experimental method would be necessary to denude the area for the beginning of development (see Wilson, '26).

8. LIFE SPAN AND RATE OF REPLACEMENT

Fraser and Smith ('28) found the age of the majority of Paphia was seven years, though a few were evidently ten years old. The same authors studied Saxidomus; the majority were about nine years old and a few sixteen years old. Approximately half of the clams breed at the end of the third year, the remainder in the fourth year. Such information is important as a basis for understanding community development, weather effects, etc. The other species of this community do not appear to have been studied. The life histories of the worms and gasteropods are quite unknown. Some Zostera-inhabiting snails of the Danish waters are annuals (Blegvad, '28).

9. PHYSIOLOGICAL CHARACTERS

Most of the experimental studies of important species from this community have been made on fishes. Among the fishes studied by the writer (1918) was the black spotted flounder (*Psettichthys melanostictus* Gir.), the remarkable resistance of which has already been noted in connection with the Pandora-Yoldia biome in which it occurs at times. As compared with Cymatogaster (Shelford, '18), it was three times as resistant to CO_2 and fifty times as resistant to H_2SO_3. This is in keeping with its habit of burying itself in the bottom. These experiments bring out the difference in physiological characters in accord with habitat and habits. This particular set indicates difference in the level occupied. In another group of experiments (Shelford and Powers, '15) the sole, *Lepidopsetta bilineata* (Ayres) was compared with *Oligocottus maculosus* Gir. Both were much more resistant to H_2S than the herring, but Oligocottus a little more resistant than the soles. The starry flounder, *Platichthys stellatus* (Pallas), takes on the color of the background after about 6 days, the results being fully as clear as in the flat fishes studied by Mast ('14). Cymatogaster responds to water conditions selecting water of pH 7.8 or 8.0 (Powers, '21). Andrews ('25) demonstrated that the young fishes of this species are much more sensitive to adverse conditions than the adults. All these facts have a bearing upon the abundance and habitat relations of the species.

10. SUCCESSION TO LAND

Where there are physiographic changes which lead to deposition or the enclosing of small arms of the sea, succession from the sea to land occurs. This is in fact the invasion of the sea area by the terrestrial climax of the region and is to be understood as of the same character as the tension between various other biomes. It is evident that this succession does not, in all cases, present the same or even similar stages between the Macoma-Paphia community and the first coniferous trees representing a terrestrial subclimax. Some of the strictly marine communities appear to indicate a trend toward land.

Haminoea, snail, and Epiactis, sea anemone, and Cymatogaster, the viviparous perch, are most abundant over muddy bottoms in protected bays and lagoons containing eel grass and not draining at low tide and appear to characterize this community. Most of the Macoma dominants are, however, present. The nearly enclosed tide-pool described by MacLean, page 319, probably represents a late stage following the Cymatogaster-Haminoea facies. (Macoma-Haminoea associes of Shelford and Towler, '25).

The suggestion that the Macoma-Upogebia facies (associes of 1925) is a forerunner of land stages appears less certain than at first. It is, however, certain that this tension line between sea and land communities prevents several intermediate types.

C. Strongylocentrotus-Argobuccinum Biome

1. depth and other conditions

This biome occurs in 0 to 225 meters and is characterized by large echinoderms (Bush, '21), large snails, and pectens (Oldroyd, '24). A total list of possible dominants and influents would be a long one. Shelford and Towler ('25) listed only a small number of these that appeared to be of uniform occurrence and conspicuous in their characteristics. With the exception of a few that live under rocks, this community is characterized by animals that live on rather than in the bottom. Petersen would have characterized the Macoma-Paphia and Pandora-Yoldia biomes as characteristically "in-fauna," and the Strongylocentrotus-Argobuccinum biome as "on-fauna."

The submarine climate in this area is quite different from that of the Pandora-Yoldia area. The difference is most pronounced at the bottom. The salinity is higher, hydrogen ion concentration (Powers, '21) is higher, the plankton is less abundant, and, as was pointed out on page 267, the penetration of light is greater in summer, than in the Pandora-Yoldia area. It is doubtful, however, if light is an important limiting factor as regards the more important influents and dominants. Another important difference between the two communities is the presence in the Strongylocentrotus-Argobuccinum community of a much greater quantity and variety of large algae. Most of the red and brown algae require shells, or solid rock and stones for hold-fasts.

Probably the most important climatic factor is the circulation of the water due to tides. The community is composed of animals on the bottom and visiting the bottom. Much of the bottom is swept clean by rapid water movement. It is only in pockets that detritus has an opportunity to come to rest on the bottom and remain longer than the periods of minimal tidal fluctuations.

The work of Wismer and Swanson (Part II) has shown that the dominants and influents of this biome occur in the pockets and protected places, but are mixed with a very few of the Pandora-Yoldia dominants and a few related species of similar habits as, for example, a different species of Yoldia.

Some of these areas doubtless are permanent due to topographic conditions and represent faciations of the biome. Others, however, are subclimax areas which, with continued deposition will build up to a point where the retention of only coarse materials and shells will exclude species belonging to softer bottom, and hence, make the community quite typical of the average of the biome.

Three earlier studies of this community added to our general knowledge. Perry ('16) made an intensive study of a strip of bottom from high tide to 156 meters and showed the results in a table[8] indicating depth and abundance. The paper by Steggerda and Essex ('25) tended to show the widely distributed species.[9] H. Andrews ('25) made an important contribution in his study of kelp. Kirsop ('22) did the first bottom sampling and contributed important records.

2. BIOME PREVALENTS OR PREDOMINANTS

A. *Dominants and Slow-Moving Influents*

The figures indicate the number of individuals per 10 m_2. These are generally distributed throughout the biome.

Strongylocentrotus drobachiensis Mül., green sea urchin; 40-200.
Argobuccinum oregonensis Red., large snail; 2-50.
Balanus nubilis Dar., barnacle; 5-50.
Balanus pugetensis Pils., barnacle; 10-400.
Balanus rostratus Hoek, barnacle; 10-400.
Calliostoma costatum Martyn, snail; 2-60.
Psolus chitonoides H. L. Clark, sessile cucumber; 1-10.
Trichotropis cancellata Hinds, snail; 2-150.
Pecten hericius Gould, scallop; 15-1000.
Pododesmus macroschisma Desh., rock oyster; 2-50.
Amphissa columbiana Dall, snail; 5-85.
Orthasterias columbiana Verrill, starfish; 1-2.
Crepidula nivea C. B. Adams, slipper shell; 10-50.
Calyptraea fastigiata Gould, chinese hat; 3-6.

B. *Biome Prevalents Differing Markedly in Importance With Depth*

Strongylocentrotus franciscanus (A. Ag.), red sea urchin, locally important, 0-36m, but secondary, 36-125m; 4-60.

[8] In this paper for 'Balanus balanoides' read *Balanus cariosus*
'Balanus aquilla' read *Balanus nubilis*.
[9] In this paper for 'Islandis borealis Gil' read *Icelinus borealis* Gil.

Stichopus californicus Clark, large cucumber; few deeper than 35m; 5-30.
Modiolus modiolus Linn., deep water mussel; 10-3000.

C. *Biome Influents*

Icelinus borealis Gilb., northern sculpin; regularly present.
Myoxocephalus polyacanthocephalus (Pallas), giant sculpin.
Rhyamphocottus richardsoni (Gunther), gruntfish.
Hyas lyratus Dana, lyre crab; 2-10.
Cancer oregonensis Dana, small cancer crab; 1-20.
Oregonia gracilis Dana.
Pandalus danae Stimp.

D. *Characteristic Species Distributed Throughout but Few in Numbers.*

Styela stimpsoni Ritter, red tunicate.
Munida quadrispina Benedict, shrimp crab; wanting 1926-28.
Crago munita (Dana), shrimp.
Spirontocaris prionota (Stimp.), shrimp.
Hapalogaster mertensii Brandt, crab.
Pagurus kennerlyi (Stimp.), hermit crab.
Purpura foliata (Mart.), snail.

3. ASSOCIATIONS

In the earlier work (Shelford and Towler, '25) two associations were recognized, one from 0 to 35 or 50 meters and the other below this depth. Muenscher ('15) has discussed the algal communities as separate from the animals.

A. *Strongylocentrotus-Pugettia*[9a] *Association*

The biome prevalents (see page 281) occur mixed with those listed below.

(1) Dominants and slow moving influents of relatively uniform distribution: Figures are number per $10m^2$.
Cucumaria miniata Brandt, red cucumber; 2-20.
Cucumaria chronhjelmi Theel, cucumber; 2-30.
Crepidula adunca Sowerby, slippershell; 10-300.
Puncturella cucullata Gould, limpet; 3-6.
Petrolisthes eriomerus St., porcelain crab; very common near shore.

(2) Influents.
Ascelichthys rhodorus, J. & G., red-finned sculpin.
Aspicottus bison Gir., buffalo sculpin.
Sebastodes sp., rockfish.
Hexagrammos (Chiropsis) decagrammus (Pall.), 10-lined greenling; common.

[9a] This was called Strongylocentrotus-Cucumaria in 1925.

Blepsias cirrhosus (Pall.), silver spot cirrated sculpin.
Odontopyxis trispinosus Lock., pitted sea poacher; common.
Myoxocephalus polyacanthocephalus (Pall.), great sculpin.
Eumicrotremus orbis (Gunther), warty lump sucker.
Caularchus macandricus (Gir.), cling fish; common.
Pholis ornatus (Gir.), chameleon blenny; common.
Pholis laetus (Cope), chameleon blenny; common.
Bryostemma decoratum J. & S., decorated blenny.
Lophopanopeus bellus St. Roth., black clawed crab; abundant near shore.
Pugettia gracilis; graceful kelp-crab.
Epialtus productus (Ran.); decorator crab.

(3) Characteristic species.
Doriopsis fulva MacFarland, lemon-colored nudibranch.
Polypus hongkongensis Hoyle, devil fish; occasional.
Cryptochiton stelleri (Mittendorff), giant chiton.
Hinnites giganteus Gray, rockpecten.
Evasterias troschelii (Stimp.), starfish; regularly present.
Acmaea mitra Esch., tall limpet.
Ischnochiton interstinctus Gould, striped chiton.

(4) Faciations and Lociations of the Association.

The reader must understand that the figures given are meant to be estimates of the average over several hundred square meters; at maximum and minimum abundance. It must further be recognized that in years of minimum no representatives of several species will be found in some areas. Such of these variations as are large are called faciations. Faciations are usually associated with differences in bottom or water circulation while lociations depend upon minor features such as accidents of "seeding," early survival, etc. (Rice, page 293). The general character of her conclusions renders discussion of lociations useless.

a. Algal Faciations

One type of faciation dependent upon bottom, is described by Wismer and Swanson, p. 333. Others occur in reduced salinity. Perhaps the most important faciations are produced by the addition of the brown and red algae to the communities. These have commonly been treated as groups of dominants just as land plants are (Muenscher, '15), but the writer ('30) has pointed out the weakness and failure of this viewpoint in the Puget Sound in the following terms:

1. Algae are not present throughout the year and often constitute seasonal societies only.
2. They do not control the presence of the dominant animals but merely influence their numbers in some cases.

3. They are not uniformly distributed but occur only in small areas.
4. Very few or no influent and important animals are limited to them; those commonly found upon them are also on eel grass (Zostera). The influence of large plants is even less in the intertidal than in the subtidal areas.

Nereocystis-Laminaria (Melanophyceae)-Lacuna Faciation.

The brown algae constitute what has long been known as the "Laminarian Zone." The Algae were studied quantitatively by Gail (Shelford and Gail, '25) near Friday Harbor. The following species were taken, five or more plants per m²: The faciation appears locally between 0 and 15 or 20 m, with all the biome and association predominants listed on page 282 present with the algae. The following are the more important algae. The figures following the name show depth limits in meters.

Nereocystis luetkeana (Mert.) Post. and Rupr., 1-15; *Laminaria* sp., 1-20; *Alaria* sp., 1-20; *Agarum fimbriatum* Harv., 5-20; *Desmerestia media* (Ag.) Grw., 1-15; *Desmerestia ligulata* (Lightfoot) Lamour, 5-30; *Costaria costata* (Turn.) Saunders, 1-20.

Animal species associated with the kelp (Nereocystis):

Lacuna porrecta Carp., snail.
Lacuna divaricata Fabr., snail.
Caprella sp. amphipod.
Pentidotea resecata (Stimp.) isopod.
Margarites succinctus Carp., snail.
Epiactis prolifera Verrill, sea anemone.

The animals of the holdfasts of Nereocystis were studied by Andrews ('25). Practically all of the species found by him were regular inhabitants of the other parts of the habitat of the Strongylocentrotus-Pugettia Assotion.

Dasyopsis-Halosaccion (Rhodophyceae) Faciation.

The red algae are distributed in patches and are most important in the lower half of the depth belt occupied by the Strongylocentrotus-Pugettia Association. There is a relatively wide area in which the brown and red algae are mixed. The animals seem not to show a difference corresponding to the different kinds of algae, but all the wide ranging biome prevalents as well as those characteristic of the association occur. Certain mud-bottomed areas well supplied with shells frequently show large masses of algae. Occasionally crabs, shrimp and blennies show a deep red color corresponding to that of the algae, which color is not characteristic of other individuals of the same species occurring elsewhere (Gamble, '10).

The algae (Rhodophyceae) of this faciation as studied by Gail (Shelford & Gail, '22) are the following. Figures indicate depth limits in meters.

Dasyopsis plumosa (Harvey & Bailey) Schmitz, 5-30; *Halosaccion glandiforme* (Gmelin) Ruprecht, 10-30; *Callophyllis* sp. (possibly *furcata* Farlow, 5-25; *Nitophyllum latissimum* (Harv.), J. Agardh, 15-25; *Agardhiella tenera* (J. Ag.) Schmitz, 5-35; *Rhodymenia pertusa* (P & R) J. Ag., 5-25; *Callymenia phyllophora* J. Ag., 15-30; *Iridaea laminarioides* Bory, 5-25; *Odonthalia semicostata* (Mertens) J. Ag., 10-25.

b. Other Faciations

Cardium-Yoldia Faciation.

The mud bottom faciation described by Wismer and Swanson (page 333) is characterized by the presence of *Cardium californiense* Desh. and *Yoldia scissurata* which is an indication of mud bottom. These occur in addition to the prevalents listed on page 281.

In the following list of associated species the figures indicate the number of individuals in 10m², see data by Wismer and Swanson, p. 340.

Yoldia scissurata Dall., 10-900.
Cardium californiense Desh., 10-80.
Solen sicarius Gld., 10-30.
Nucula castrensis Hinds, 2-400.
Polinices pallida B. & S., 300-600.
Venericardia ventricosa Gld., 1-100.
Marcia subdiaphana Carp., 10-80.
Crago alaskensis Lock.

With the exception of the *Marcia subdiaphana* the species listed are in part characteristic of the ecotone between the Pandora-Yoldia Strongylocentrotus-Argobuccinum biomes as described on page 270. *Marcia subdiaphana* is an important prevalent in the Pandora-Yoldia community. *Yoldia ensifera* which is important in portions of that community, was represented by a sparse population (see pp. 269 and 344).

Pisaster Ochraceus Faciation.

Pisaster ochraceus (Brandt) is an ecotone species occurring in the very upper edge of the Strongylocentrotus-Pugettia community and in the tidal community. It is not sufficiently abundant to have any marked influence, except above the Pandora-Yoldia areas. Here there is an unusual arrangement of communities which is very important from the standpoint of the presence of various species (Fig. 4). The Pandora-Yoldia areas are characterized by mud bottom and little wave action at a depth of two or three meters, below low tide. They commonly give way to a marginal strip of poorly developed Strongylocentrotus-Pugettia community containing *Pisaster ochraceus* (Brandt) and green sea urchins. Large cucumbers, *Stichopus californicus* Stimp., and especially *Cucumaria miniata* (Brandt) in abundance, characterize this area.

This arrangement of the animals and conditions which they indicate, explains the occasional presence of stray motile species of the Strongylocentrotus community on typical Pandora bottom. An occasional *Stichopus californicus* is found on the Pandora bottoms, but is interestingly dull in color and sickly in appearance. This arrangement of communities shown in Figs. 4 and 7 is particularly important in connection with occurrence of fishes, crabs, etc. Species of fishes and crabs belonging properly to the Strongylocentrotus community are found occasionally in the shallower parts of the Pandora-Yoldia community adjacent (see pages 262 and 314).

B. *Strongylocentrotus-Pteraster Tesselatus Association*

This is mainly below 36 to 50 meters, down probably to 225 m. Since 1925 the community has been examined in the deeper waters especially down to 225 meters, south of Flat Top Island. In the deep water at and above 225 meters the wide ranging dominants remain as elsewhere except at this point and south of Turn Island where *Chrysodomus liratus* Mart., the large snail, takes the place of *Argobuccinum*.

(1) Dominants and slow-moving Influents.

(See also those listed on page 281). Figures indicate the number of individuals per 10m².

Crossaster papposus (L.) M. & T., rose star; 3-6.
Pteraster tesselatus Ives, cushion star; 2-4.
Gorgonocephalus eucnemis M. & T., basket star; 1-3.
Terebratulina unguicula Carp., brachiopod; 10-30.
Hemithyris psittacea Gmel., brachiopod; 10-20.
Evasterias acanthostoma Verrill, star fish.
Ptilosarcus quadrangularis Moroff, sea pen; 2-4.
Aglaophenia struthionides (Murray), ostrich plume hydroid.
Pecten hindsii Carp., scallop; 5-100.
Modiolus modiolus Linn., deep water mussel.

Pectens and barnacles are more abundant and *Stichopus californicus* is usually less abundant, than in the shallower water association.

(2) Influents.

Gilbertidia sigolutes (J. & S.), Gilbert's sculpin; common.
Microstomus pacificus (Lock), smeardab.
Nautichthys oculo-fasciatus Girard, sailor fish.
Asterotheca alascana (Gilbert), rat-tail fish; Alaskan seapoacher.
Pandalus stenolepis Rath, shrimp.
Pandalus borealis Kröyer, pink shrimp; common.
Pandalus montagui tridens Rath., Montague's shrimp.
Pandalus jordani Rath., Jordan's shrimp.
Chorilia longipes Dana, crab; 2-10.

The biome dominants and influents extend throughout, mixed with the association influents and dominants. The climate is characterized by lower temperature, less light, more constant conditions, and less plankton and floating detritus, than that of the Strongylocentrotus-Pugettia association.

(3) Faciations.

Faciations occur in this association due to differences in circulation, bottom materials, etc.

a. Modiolus Faciation

Under certain submarine climatic conditions, chiefly below 35 m and down to 225 m and below, *Modiolus modiolus* (Linn.) occurs as an important dominant in the Strongylocentrotus-Argobuccinum biome. A similar community is important in the North Atlantic (Sparcks, '29). In San Juan Channel there are areas in which this species occurs covering mud or clay bottoms, usually in depressions protected from tidal currents. These appear to be areas in which Modiolus is a true dominant and the community is at least two-layered, sometimes possibly three-layered. The probable layers are composed of animals (1) *on* the Modiolus, (2) *among* the Modiolus and (3) in the mud *below* them. Worms live below the Modiolus.

Modiolus appears to occur in solid masses of 2,000 or more on ten square meters. The beds do not appear to be continuous and estimates of 3,000 to 4,000 per $10m^2$ are about the maximum. They do not occur on all muddy bottoms and become very scattered at and above 35 meters depth (Wismer and Swanson, page 340.

All the principal dominants and more important influents belonging to the entire biome and those restricted to the Strongylocentrotus-Pteraster association occur through the area controlled by Modiolus. Modiolus supplies the substratum necessary for their attachment and they are often quite abundant. It is not clear from the investigation what lociations occur or the difference between this and the climax on mud below dead shells. A number of worms have unfortunately not been identified. Some of these, scaly worms (Polynoidae) and the sea mouse (Aphroditidae), which are perhaps characteristic, and Nereidae, are present.

4. EXTENT AND RANK

This community occurs on the west coast of Oregon, Washington, and Vancouver Island and evidently covers much bottom quite continuously. Its general range is unknown but its occurrence on the west coast of Vancouver Island in Barkley Sound was indicated by shore examination and a small amount of dredging with a small naturalist's dredge operated by hand in 1930. This locality is on the open shore of the Pacific. The water is subject to considerable dilution by the heavy rain of the coast especially in winter. The wave action is that of the open ocean coast. The following species were well represented:

Strongylocentrotus drobachiensis O. F. Mul., green sea urchin.
Strongylocentrotus franciscanus A. Ag., red sea urchin.
Balanus nubilis Dar., large barnacle.
Pugettia gracilis Dana, graceful kelp-crab.
Ischnochiton radians Carp., chiton.
Ischnochiton mertensii Midd., red chiton.
Lepidochitona ruber Linn., chiton.
Amphissa columbiana Dall., snail.
Margarites pupillus Gould, snail.
Calliostoma canaliculatum (Martyn), snail.
Crepidula orbiculata Dall., slipper shell.

There are, doubtless, associations covering a part of the range, as well as those recognized as dependent upon depth. In its contact with the Pandora-Yoldia biome, the boundary is sharp and the ecotones narrow. The boundary between this community and the Macoma community is wide in proportion to the width of the latter, being equal to one half or more of the width of the Macoma-Paphia biome.

5. INTERACTION IN THE BIOME

The great variety of large organisms which make up the dominants and influents of this community make possible many inferences as to interaction from the general habits of these species.

A. *Coaction*

One of the most important coactions was studied by Weese ('26) who worked on the food of an important dominant, the green sea urchin. Its food included more than fifty per cent plant material, chiefly fragments of plants growing in shallow water. Animal food included Balanus, Bryozoa, sponges, and hydroids.

The considerable number of sea urchins present and the action of these in scraping the smaller plants and animals from the substratum is important (Weese, '26). The various starfishes play an important rôle. Though present in small numbers, their large size renders them potent attackers of barnacles, which are present in some abundance also. They also feed upon other forms. Argobuccinum, Calliostoma, Amphissa, and other snails probably prey upon the sedentary species. Very little is known of the food of the crabs and fishes. Snails supply shells for hermit crabs, etc.

B. *Reactions and Succession*

The surface of nearly all rock is encrusted with bryozoans, shells of barnacles, rock pectens, serpulids, etc., and, in the shallower water, the bodies and hold-fasts of algae. The loose skeletons of molluscs, barnacles, and

echinoderms form beds of considerable extent in pockets swept by currents. In many places with bottom of fine materials, the shells of mollusca form important places of attachment for barnacles, chitons, and algae. The detritus from algae and Zostera, etc., is important as food for animals and as a part of the floating materials influencing the marine climate.

Mud and sand lie in depressions in the bottom. Such physiographic inequalities are gradually eliminated by current action which fills the depressions. When nearly filled shells and other coarse materials are deposited and mud bottoms become covered with shells. The mud bottom faciation is succeeded by the typical composition of the association.

6. PHYSIOLOGICAL CHARACTERS

A long series of experiments by the writer ('16)[10] was concerned with resistance to temperature and fresh water. The shrimps which occurred in great abundance were above 30m and were two or three times as resistant to freshwater at a temperature of 24°C. as shrimps below 30m. The 30m line roughly marks the division between two associations. However, scattered individuals of shallower water shrimps found in deep water were also less resistant but at the same time more resistant than the species largely confined to the deeper water. The same general principle holds good for the crabs and echinoderms.

The series of experiments brought out radical differences between the Balanus-Littorina and Strongylocentrotus-Argobuccinum biomes through the comparison of similar species of barnacles, mussels, etc.

D. BALANUS-LITTORINA BIOME

This community is associated with the Macoma-Paphia biome and there has been some confusion. The relative levels at which these two biomes occur must be clearly in mind. In those parts of the area of study where the tidal range in level (as indicated by animals) amounts to about 3m, a hard substratum is completely occupied by the Balanus-Littorina biome. The Macoma-Paphia biome, however, rarely reaches above 1½m below the higher tides, or, in other words, overlaps about half the belt of the Balanus-Littorina biome. The Macoma biome extends downward at least 8m below the lower limit of the Balanus-Littorina biome. Where there is a suitable upper shore substratum the Balanus-Littorina biome is to be expected above the Macoma-Paphia biome. Rocks imbedded in tidal Macoma sands are commonly covered with tidal Balanus and associated forms. In other cases where there is not much deposit of sand, the higher portions of a beach are often gravel and are covered with Balanus and Mytilus. Occasionally the two may overlap with the Macoma beneath ("in-fauna") and the Balanus above ("on-

[10] In this paper for *"Balanus balanoides"* read *Balanus cariosus* (Pallas) and for *"Balanus aquilla"* read *Balanus nubilis* Dar.; transpose "All alive" and "All dead" after first two species in Table 5, p. 167.

fauna"). Thus the two intermingle like grassland and forest to make a park land savanna.

The presence of Balanus-Littorina species on fine gravel or sand is, as much or more a matter of general hydrographic conditions as of substratum. Even fine sand beaches in protected bays frequently have their higher reaches partially covered with *Mytilus edulis* which forms a substratum to which *Balanus glandula* is attached.

This community is strictly tidal on the north Pacific shores examined. It is normally exposed throughout its extent at medium low tide and it, together with a considerable area of the community below, is exposed at the extreme low tide. Peculiarities of the arrangement of the species within this biome throw much light on the general question about communities. It has been more thoroughly studied than any of the major communities of the waters under consideration. The work done by Shelford and Towler ('25) included a reconnaissance of the shore over a considerable distance shown in their maps (pp. 48-50). At the outset they recognized several degrees of community luxuriance, one or two in addition to those indicated on the map on page 53, but part of these had to be dropped. This was due to the fact that in making the reconnaissance over 132 km (80 miles) of mainly broken coast, it was not possible to identify barnacles beyond the point of determining that the *Balanus cariosus* was almost universally present on stationary objects. Since that time, studies of barnacles by Towler ('30), Worley ('30), and Rice ('30) have shown that in enclosed bays, inner ends of coves, etc., *Balanus glandula* Dar. increased and *Balanus cariosus* (Pal.) decreased, especially in the upper portion of the community. On the whole Worley found *Balanus cariosus* was more abundant in waters of lower salinity, and larger in waters of higher salinity. Rice concluded that low salinity favored a great abundance of barnacles on reefs offshore, the greatest abundance being in 26-28 gm. per 1. The relations as observable at any time are likely to be contradictory because of their determination by a series of events at the time of seeding.

1. Associations and Faciations

Shelford and Towler not only evaluated the grades of the Balanus-edulis association which we call *faciations* in this paper, but two associations were recognized. In 1929 after a trip to Alaska and Southern California in which barnacles were collected, an attempt was made to clarify these two associations. The writer was not able to identify all the barnacles in place and from the collections made, *Balanus hesperius* Pils. was given a place not justified by the observations at La Jolla by Rasmussen. Rasmussen found that three of the principal species are different at La Jolla and in the Pugent Sound region. In Southern California *B. cariosus* is not numerous and never dominant. It has no equivalent except possibly *Tetraclita squamosa rubescens* Dar. The

place of *Chthamalus dalli* is taken by *C. fissus* Dar. and that of *Littorina sitchana* and *L. scutulata* by *L. planaxis* Phil. The suggestion of a Mitella-Mytilus association in 1930 has not been justified by subsequent observations. An unusually definite and significant arrangement of the dominants was found at Barkley Sound (station 23 and 24).

A. *Balanus-Mytilus californianus Association*

In Barkley Sound (west coast of Vancouver Island) the arrangement of the predominants of the Balanus-M. californianus association on one of the Chain Islands (Holy Island) was very illuminating. Here on the outside of the island facing the open Pacific the principal dominants of the community as a whole are arranged in very definite faciations on slopes and vertical cliffs. These are four in number, arranged as shown in the Table 4. The principal dominant in each faciation is named first.

TABLE 4. LIST SHOWING THE FACIATIONS OF THE BALANUS-M. CALIFORNIANUS ASSOCIATION IN BARKLEY SOUND

Opposite the name of the species is the average per m^2.
Balanus-californianus Association, 190 cm. wide.

1. Littorina-glandula Faciation, 20 cm wide.	
Balanus glandula Dar., barnacle	2400
Littorina scutulata Gould, snail	200
2. Littorina-cariosus Faciation, 45 cm wide.	
Balanus cariosus (Pallas), barnacle	3140
Littorina scutulata Gld., snail	228
Acmaea digitalis umbonata (Nutt.), roe limpet	70
Thais emarginata Desh., snail or whelk	38
3. Mitella-Mytilus Faciation, 65 cm wide.	
Mytilus californianus Conrad, California mussel	1943
Mitella polymerus (Sow.), goose neck barnacle	1506
Balanus cariosus (Pallas), barnacle	1363
Red sea anemone	120
Littorina scutulata Gld., snail	225
Littorina sitchana Phil., snail	50
Thais emarginata Desh., snail or whelk	180
Acmaea digitalis umbonata (Reeve), limpet	110
Acmaea cassis Esch., limpet	380
4. Cribrina Faciation, 60 cm. wide.	
Cribrina xanthogrammica (Brandt), green sea anemone	3140
Balanus cariosus (Pall.)	4
Chitons	40
Pisaster ochraceus (Brandt), common starfish, an ecotone species	6
Mytilus californianus Con., Calif. mussel	20
Chthamalus dalli Pils.,[11] small barnacles	3000

In the Mitella-Mytilus Faciation area, *Mytilus californianus* is a true dominant, as it covers rock surface and quite completely excludes *Balanus cariosus*. Individuals of this species were small and seated on the shells of the *Mytilus californianus*. The arrangement appears to be similar to that observed by the writer at Taft, Oregon (Shelford, '30). It appears that this arrangement may be quite common on the wave-swept headlands of a con-

[11] Chthamalus does not average this density over the area but occurs in local clans having about this number per m^2.

siderable part of the coast of Vancouver Island, Washington, Oregon, and perhaps northern California.

B. *Balanus-Mytilis edulis Association*

Fifteen meters from the point described in Table 4, around the north side of Chain Island, *Mytilus californianus* gives way to *Mytilus edulis* Linn., first at the top and finally throughout its zone. The definite arrangement of the species making up the communities disappears and they become quite generally mixed together. On the inside of the island all definiteness of arrangement disappears. The inside is exposed less to wave action and more to fresh water while the outside is definitely exposed to the surf and waves. The writer recognizes only the two associations originally described by Shelford and Towler ('25).

A few miles west of Port Angeles, Washington, all the principal species of the biome appeared on the same shore and were quite generally mixed together. This is on the south shore of the Strait of Juan de Fuca and in the transition between the communities which may contain Mitella and *Mytilus californianus* as important general dominants and those in which the former occurs in clans and the latter is not abundant. Likewise Clements (personal communication) finds that all the principal dominants of the deciduous forest occur together in certain parts of Kentucky, though in other places they are separated into three associations: oak-hickory, beech-maple, and oak-chestnut, each with a rather large distribution area. Some of these are separated into consociations as for example: a *beech consociation.*

2. LOCIATIONS

A. *Tide Pools*

Tide pools have received much attention on account of the ease with which they may be studied. Tide-pools which lie within the intertidal community level are usually lociations of the tidal community (Gersbacher and Denison, '30) except where the bottom is sand. Sand-bottomed pools with rock walls are not common. The usual rock-bottomed tide-pool contains both common species of Balanus, the two species of Littorina, also Mytilus, limpets, hermit crabs and snails which frequent the tidal area and are regularly found out of water at low tide. In addition, fishes which stay near the water margin and hence are quasi-residents of the biome. To these are added a few sub-tidal animals such as a Cucumaria, serpulids, and occasional snails and chitons.

B. *On Rock Faces*

Variations in the arrangement of dominants and influents on relatively similar shores are due to mere local conditions and the effect of weather, tide, etc., during the early part of the individual life-history.

DYNAMICS AND EXTENT OF BOTTOM AND SHORE COMMUNITIES

By

LUCILE RICE, D. I. RASMUSSEN, V. E. SHELFORD, A. O. WEESE, ARCHIE MACLEAN AND H. C. MARKUS

I. BALANUS-LITTORINA BIOME

A. FACTORS CONTROLLING ARRANGEMENT OF BARNACLE SPECIES IN TIDAL COMMUNITIES

LUCILE RICE

Several papers have been written in regard to the distribution of tidal barnacles in the Puget Sound region. Shelford ('30) and Towler ('30) indicate that they group themselves into definite communities, and Worley ('30) and Rice ('30) indicate that low salinity favors abundance, seeding and the survival of young barnacles.

Very little is known about the rate of seeding, conditions controlling the survival and the time of most abundant seeding. Pierron and Huang ('26) whose observations covered the period from June 20 to August 2 only, state that the greatest attachment upon denuded rocks just off Brown Island occurred early in July, and that a few died after each period of attachment. Johnson (unpublished) shows that March, April, May, August, September, October 1929-30 were the months of most abundant survival of young barnacles on rocks and pilings under the pier at Friday Harbor. These authors did not determine the species.

The purpose of this study was (1) to check the abundance of mature barnacles at some of the stations observed in 1928 (stations 1-15) (Rice, '30); (2) to check on the survival and abundance of young of the different species (June 17 to August 18, 1930); and (3) to throw further light on the effects of pollution, weather, type of bottom, tide, and salinity upon the survival of young barnacles. To accomplish this stations 16 to 22 were added.

The species considered are *Balanus cariosus* Pal., *Balanus glandula* Dar., *Chthamalus dalli* Pils., all of which are tidal.

Actual counts of young barnacles per dm² were made at the first (top), second (middle), and third (bottom) meter levels of the tidal area and when possible the species were identified.

1. FLUCTUATIONS IN NUMBER OF YOUNG BARNACLES WITHIN SHORT PERIODS

Fifteen stations were established. The more important were observed at approximately ten day intervals, others less frequently. Some of the stations located on the salinity map of Shelford ('30) were used again.

A. *High salinity and rough water station*

(1) Seeding and survival on undisturbed rocks.

This station (station 12) was in an area of the highest salinity (30 gm per 1) with continuously rough water available. It was located on a rocky point at Kanaka Bay and got the full force of the waves and incoming tides from the ocean through the Juan de Fuca Strait. The rocks were either abrupt or gradually sloping and exposed to the sun when not covered by the tide.

Along with the plots mentioned an area of barnacles 1 dm^2 was carefully outlined with white paint and all barnacles plotted and counted. All dead were picked off each time. From these areas estimations were made for Fig. 5.

It was noticeable in these marked areas that with the exception of *C. dalli,* the young which attached to the old barnacles had a much better survival than those which attached to the bare rock.

The older barnacles, ranging in diameter from 10 mm to 40 mm held constant throughout the period and were distributed in levels as follows: 1st meter below average high tide *B. cariosus* 1000 per m^2; 2nd meter *B. cariosus* 8000 per m^2; 3rd meter *B. cariosus* 2500 to 3000 per m^2; a few *C. dalli* scattered through the second and upper half of the third meter; no *B. glandula* at any level.

Fig. 5 shows the total population at station 12, rate of attachment, survival and death rate by species of the young barnacles for six observations made from June 21 to August 11, 1930.

The young barnacles at all three meter levels for the first observation, June 21, were *B. cariosus* from 1 to 5 mm in diameter; most of them were 5 mm or more showing that they were several weeks old.

The second observation showed a heavy attachment of all three species. Most of the *B. cariosus,* observed during the first period, were living and had increased in size approximately 1 mm.

The third observation showed a high death rate and a few attachments by both *B. cariosus* and *B. glandula* in the first and second meter levels, and an increase in the third meter. *C. dalli* increased greatly in the first and second meters.

The fourth observation showed many dead *C. dalli* followed by great increase during the period to the fifth and sixth observations. Every available space was densely set with them. They do not very often attach to other barnacles. *B. cariosus* held fairly constant during the third period (fourth observation) and increased during the fourth and fifth periods. All of the *B. glandula* in the third meter died, increased again at all three levels during the fourth period, to die again at the second and third meter levels during the fifth period.

The following percentages of the three species of young barnacles present June 21 were living August 11; first meter *B. cariosus* 3%, *B. glandula,* 0%, *C. dalli* 0%; second meter *B. cariosus* 10%, *B. glandula* 5%, *C. dalli* 0%; third meter *B. cariosus* 15%, *B. glandula* 0%, *C. dalli* 0%.

This percentage of survival of young barnacles compares rather favorably with the number of mature barnacles found at the same levels. From a study of the small percentage of survival of young as seen by Fig. 5 and from others observations made on nearby areas it is made evident that barnacles attached to unprotected surfaces after the first or middle of June had little chance of survival during the warmer weeks of July and August.

Barnacles more than 10 mm in diameter at the first observation (June 21) were not enumerated in the counts used in the graphs. These older barnacles changed very little in abundance but increased in size from 10 mm to 15 mm during the seven weeks.

(2) Seeding and survival on denuded and planted rocks.

At the first observation, June 21, an area of 1 m^2 was cleared at all three levels by removing both the old and the young barnacles. In addition to this, rocks from land were placed out at one, two and three meters below high tide. The young barnacles did not survive on these planted rocks suggesting that the effects of other organisms may be essential. They attached and grew as large as 0.5 mm to 1 mm in diameter but were dead at the next observation, with the exception of a few which attached to the under side of one of the rocks. On the cleared area at the third meter level one sixth of the new sets of *B. cariosus* survived at the end of each period and were not included in the graphs.

B. *High salinity—Quiet water Station*

Fig. 6 (station 8, located on the east side of Brown Island) shows the fluctuation of young barnacles in a well protected area. The salinity here is 29 gm per 1 and there is very little wave action. This figure compares very favorably with Fig. 5 for survival and death rate except for the last two periods. During the week prior to July 28, a great amount of oil ran into the bay and apparently killed all of the young barnacles. At any rate all of the barnacles on July 28 were very young measuring 0.5 to 1 mm in diameter; and many of these did not survive the hot weather and low tides from July 28 to August 8.

Areas which had a heavy covering of Ulva examined on August 8 showed a heavy stand of young barnacles measuring in diameter from 2 to 10 mm. These were well protected from sun, and the oil which collected on the plants, did not get through to the rocks below.

(1) Effect of tides and weather.

When Figures 5 and 6 are compared the periods of most abundant seed-

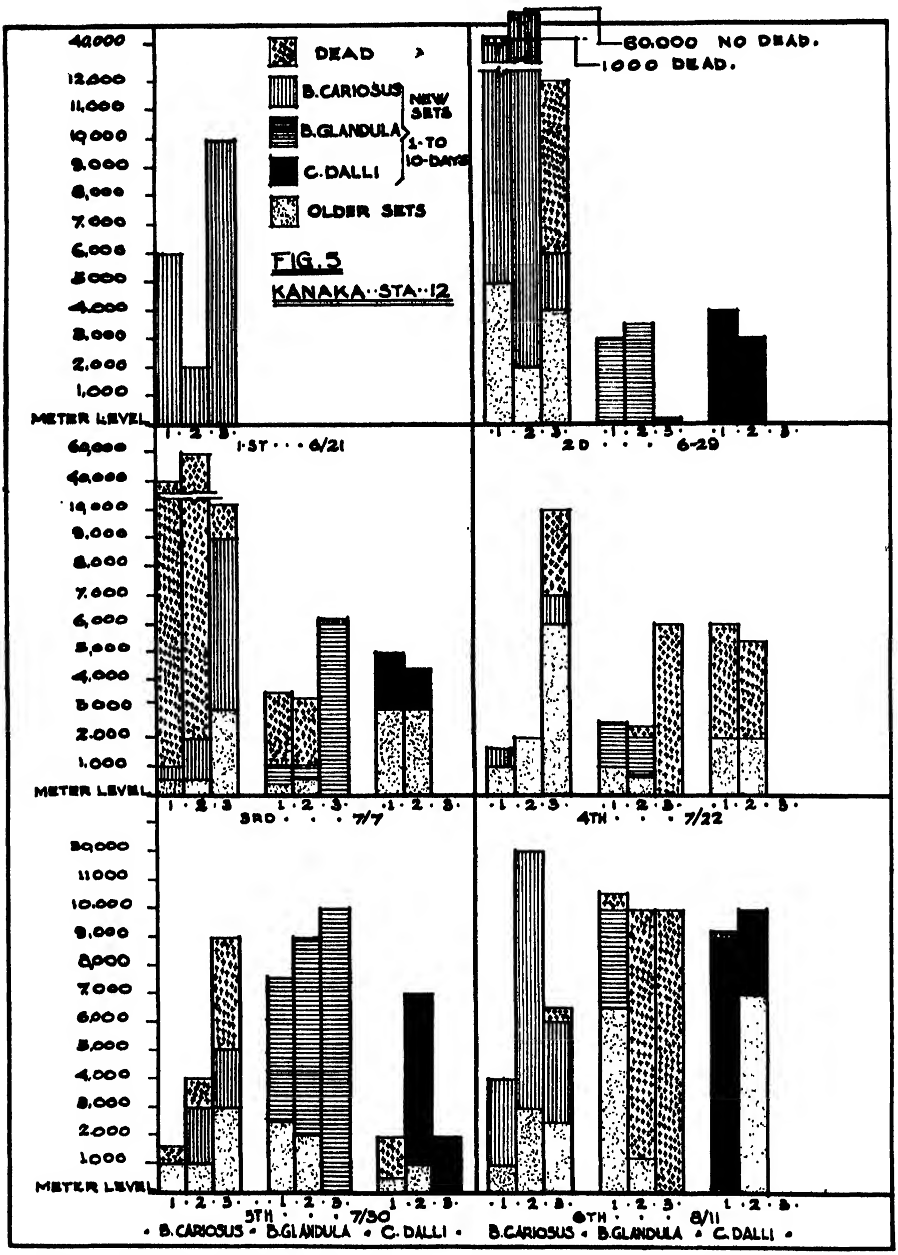

FIG. 5. Showing the total population, rate of survival, attachment and death of young barnacles per m² over three vertical meters of shore which are covered and uncovered with the average change of tide. High tide is zero. The horizontal scale is in meters below high tide, the vertical scale is in numbers of individuals per square meter. Data are for six periods of approximately ten days each, from June 21 to August 11 at Kanaka Bay (station 12), rough water, high salinity (30 gm per 1).

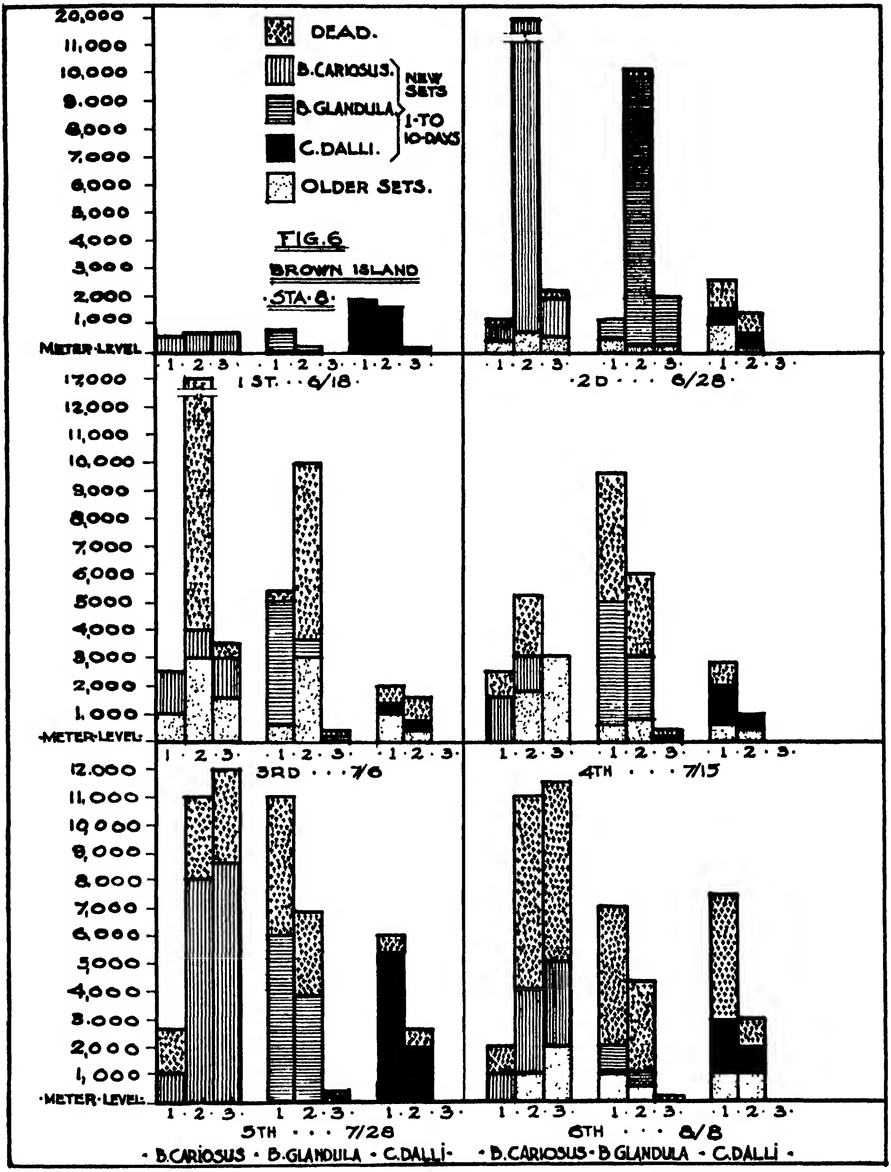

FIG. 6. Similar to Fig. 5 with same legend. Data for six periods of approximately ten days each, June 18 to August 8. Brown Island (station 8) quiet water, high salinity (29 gm per 1). Lack of survivals of all species at the fifth observation is probably due to a large amount of oil poured into the harbor during this period.

ing for a given area are found to run in cycles. Seeding and survival of the different species fluctuate considerably at different levels.

From a study of these two, Figures 5 and 6, and Table 5 which shows the tide and weather conditions for the whole period, it is apparent that the

heaviest seeding of the whole period took place between June 21 and June 29, through a period of the highest, and lowest of the low tides. However, the lowest tides occurred between 8 and 12 A.M. and the weather was cool and cloudy. (See U. S. Dept. of Com. Tide Tables for 1930.)

The highest death rate and poorest seeding were between June 29 and July 22. During this period the weather ranged from moderate to very hot and dry and all of the low tides came between 7:50 A.M. and 1:30 P.M. The best survival of young at this time took place in the protected crevices and at the third (lowest) meter level.

From July 22 to August 11 there was an increase in the amount of new attachments and in the survival of the old. Though the weather was dry and hot the fact that the lowest tides came between 7:00 and 11:30 A.M. and did not fall as low, apparently protected the barnacles.

Observations made at stations 12 and 8 on July 28 in plots other than those used for the graphs showed on all surfaces exposed to the sun, conditions similar to those shown in the graphs for that date. In crevices under Ulva, and on the shaded side of rocks in the second meter, numbers were estimated as 20,000 *B. cariosus* and 10,000 *B. glandula* per m² ranging in size from 1 to 15 mm. Approximately two-thirds of each were from 10 to 15 mm in diameter; the other third was 1 to 3 mm. The third (lowest) meter showed 4000 to 5000 *B. cariosus,* 1 to 15 mm, and 12 to 14 *B. glandula* 1 to 10 mm, the ratio of sizes about the same as for the center meter. Station 8 showed similar survival. The number of attachments was never at any time as great at this station as at station 12.

TABLE 5. Tides and weather condition, 1930. Heights in feet.

Date	Height of Low tide	Time	Prevailing weather
June 16–22	−0.1 to 0.5	2:00 P.M. to 6:56 A.M.	cool, cloudy
June 23– 1	−0.7 to 0.0	7:31 A.M. to 1:33 P.M.	cool, clear to cloudy
July 2– 6	1.6 to −0.3	2:23 P.M. to 7:15 A.M.	moderate
July 7–14	−0.8 to −0.3	7:50 A.M. to 11:57 A.M.	cool first part, hot last part
July 15–20	0.5 to 1.0	12:33 A.M. to 5:30 A.M.	moderate
July 21–29	−0.1 to 0.1	6:13 A.M. to 12:21 P.M.	hot, dry, bright
July 30– 3	1.6 to 0.3	1:05 P.M. to 5:54 A.M.	hot, dry, bright
August 4– 9	−0.2 to −0.5	6:42 A.M. to 9:50 A.M.	hot, dry, bright
August 11–15	0.2 to 3.9	10:54 A.M. to 1:10 P.M.	cooler

c. *Comparison of High and Low Salinity Stations*

(1) A muddy bay in a high salinity region and a muddy bay in a low salinity region.

On the northwest end of San Juan Island there is a long shallow bay known as Wescott Creek. It is two miles long and one mile wide, and has mud bottom throughout except at the entrance and ranges in depth from 1 to 10m, see (MacLean, p. 319).

The water is quite muddy most of the time, especially during tide movements but there is little wave action except during storms. Great quantities of dust from the lime pits nearby cover the water and form thick crusts over all the barnacles.

Winter conditions in this bay are not known but there is a possibility that much fresh water may come in at this time from streams at the head of the bay. During the summer there is no fresh water entering and the salinity ranges from 29 to 30 gm per liter.

Every available stick, stone and rock was covered with very large *B. glandula* and *B. cariosus* through all three levels.

First (top) meter: *B. glandula,* 1500-2000 per m², 20mm in diameter.

Second meter: *B. glandula,* 1000-1500 per m², all attached to *B. cariosus. B. cariosus,* 100 to 120 per m², 20 to 60 mm in diameter, 20 to 70 mm tall.

Third meter: *B. glandula,* 300 to 400 per m², 15 to 20 mm in diameter, covered the *B. cariosus. B. cariosus,* 50 to 100 per m², 40 to 70 mm in diameter, 20 to 70 mm tall. Almost all were old and heavily encrusted with mud. The young were very few.

In a small mud bay at Point Roberts at the mouth of the Frasier River barnacles of all species were more abundant than at any place previously observed.

The salinity of this station was not determined but it is nearer the Fraser River than the Sucia Islands about which the salinity was 26 gm. per liter.

On account of the splitting of the river by Lulu and Westham Islands fresh water carrying much sediment flows toward the Point, and into Boundary Bay, and forms large mud flats. Three miles of shallow beach may be exposed at low tide. Wave action is severe on exposed points and seems to prevent attachment except in protected spots. Here again every available stick, stone and rock was densely populated with barnacles. They were very long and slender, 2 to 4 mm in diameter and 15 mm high. The first (top) meter showed 202,800 *B. glandula* per m² growing very close together and piled on one another. The greatest abundance was on the shaded side of the rocks.

In the second meter level there were 2280 *B. cariosus* per m² 10 to 15 mm in diameter and 27 mm tall; these were covered with small *B. glandula* 3 mm in diameter and 2 mm high, 4000 per m². The third meter level had the same *B. cariosus* count and very few *B. glandula*.

C. dalli was more abundant, extending higher and lower than any of the other barnacles. Every spot not occupied by other barnacles was piled high with these barnacles. 42,400 *C. dalli* per m² were counted above the *B. glandula* line and 236,600 *C. dalli* per m² were counted below the third meter level (see Huntsman '18).

Table 6 shows that the bay at Point Roberts in an area of low salinity is

favorable for successful attachment and survival, and consequent small size of barnacles; while the bay at Wescott Creek is characterized by smaller numbers but successful individuals attain large size.

TABLE 6. Comparison of barnacles in an open mud bay with low salinity and a closed mud bay with high salinity.

Species	Meter level	STATION 22—POINT ROBERTS Low Salinity			STATION 17—WESCOTT BAY High Salinity		
		Number per m²	Size, mm		Number per m²	Size, mm	
			Diameter	Height		Diameter	Height
B. glandula...	1	202,800	2–4	15	2,000	20	30
B. cariosus...	1	0	0	0	0	0	0
B. glandula...	2	4,000	3	2	1,500	20	30
B. cariosus...	2	2,280	10–15	27	120	20–60	20–70
B. glandula...	3	500	3	2	400	30	40
B. cariosus...	3	2,280	10–15	27	100	40–7	20–70

C. dalli was scarcely noticeable at Wescott Creek but was extremely abundant at Point Roberts. It seemed that 1930 was a favorable year almost everywhere for this barnacle. It was so inconspicuous in 1928 that it was seldom considered.

Nothing is known about the environmental conditions in these bays. Gran and Thompson ('30) in a study of diatoms within the San Juan Archipelago mention that the freshwater coming in from the Fraser River is extremely favorable for the growth of diatoms.

The extreme size and abundance of *B. glandula* is noticeable at Wescott Bay while the small size and extreme abundance of both species is evident at the other station.

2. CHANGE IN COMMUNITIES IN A TWO-YEAR INTERVAL (salinity 26.5-28-0 gm per 1)

Many of the stations (salinity 26.5-28.0 gm per 1) visited in 1928 and described in the author's paper ('30) showed changes in 1930. (For station locations see Fig. 1, also map, Shelford, '30, p. 223. Station 19 unnumbered.)

A. *Blind Bay near Orcas—Station 19*

Blind Bay on the northeast side of Shaw Island has two types of shore line, long gradual sloping gravel beach on the east side and a vertical rocky cliff on the west. In 1928, all available rocks and loose gravel on the gradually sloping east shore were covered with dense masses of mature *B. glandula* through the first, second and third meter levels. The rugged rocks and vertical cliffs on the west side of the bay were set with pure stands of large *B. cariosus* 25 to 30 mm high x 20 to 30 mm in diameter with few if any young barnacles present.

An examination of these areas in 1930 showed that the mature *B. glandula* on the east beach had disappeared and were replaced by young *B. glandula,* 4 to 6 mm in diameter, with a few scattered *B. cariosus* in the lower meter. On the west rocks and cliffs all of the old *B. cariosus* were dead, many had been washed off and those remaining were heavily set with *B. glandula* in the first meter and with young *B. cariosus* in the second and third meters.

Reefs at the entrance of this bay were densely covered with both young and old barnacles, with the young *B. glandula* extending well down into the second meter below high tide and attached to the old *B. cariosus.* Star fishes and snails were very abundant in the third (lower) meter and had done considerable damage to the old barnacles in both the second and third meters.

Starfishes were abundant, 3 to 5 per m^2, at the cable crossing, a check station located on San Juan Island, northeast of the Biological Station (station 18), and at Barnacle Rock (Rice, '30; station 5). At both stations they did great damage to the barnacles in the third (lowest) meter level. They actually killed all barnacles on the third meter level at the cable crossing and did considerable damage to those in the second meter. They may help to account for the great differences in abundance of old barnacles in the second and third meters at Barnacle Rock as shown by Table 7.

B. *Barnacle Rock near Olga—Station 5*

Barnacle Rock, a rocky reef near Olga, had next to the largest barnacle population examined within the area of low salinity in 1928. Table 7 shows the change and distribution of the barnacles at each level in 1928 and 1930.

TABLE 7. Comparison of barnacle population per m^2 of Barnacle Rock. Station 5, near Olga.

	1928			1930		
	Mature	Young	Total	Mature	Young	Total
First (top) meter						
B. glandula..........	9,000	4,000	13,000	3,200	37,700	40,900
B. cariosus..........	15,000	5,000	20,000	6,500	48,000	54,500
Second meter						
B. glandula..........	20,000	3,000	23,000	0	45,400	45,400
B. cariosus..........	9,000	1,000	10,000	11,000	14,400	25,400
Third meter						
B. glandula..........	0	0	0	0	0	0
B. cariosus..........	15,500	5,000	20,000	0	21,000	21,000

The following differences are apparent between the 1928 and the 1930 observations: The number of mature *B. glandula* had decreased in the first and second meter levels; *B. cariosus* had decreased in the first and third and had

increased in the second meter; young *B. glandula* increased in the first and second meter; young *B. cariosus* had increased in all levels.

C. dalli covered all areas not occupied by other barnacles in the first and second meter levels in 1930 but was not present in noticeable numbers in 1928. The first trip to this station was made July 1 and a second trip was made August 11 to see what changes had taken place meanwhile. The only difference noticed was the increase in size of young observed on July 1, lack of dead young and the increase in number of 0.5 to 1.0 mm young.

TABLE 8. Comparison of young barnacle population per m² of high salinity and low salinity stations; August 11, 1930.

	STATION 12 High salinity; 30 gm per 1			STATION 5 Low salinity; 28 gm per 1		
	Older Sets 5–15mm	New Sets 1–5 mm	Total	Older Sets 5–15 mm	New Sets 1–5 mm	Total
Top meter						
B. glandula...........	6,500	3,500	10,000	27,700	10,000	37,700
B. cariosus...........	1,000	3,000	4,000	40,000	8,000	48,000
Second meter						
B. glandula...........	6,500	0	6,500	40,000	5,400	45,400
B. cariosus...........	3,000	27,000	30,000*	18,000	6,400	24,400
Third meter						
B. glandula...........	1,200	0	1,200*	0	0	0
B. cariosus...........	4,800	1,200	6,000	11,000	10,000	21,000

A comparison of high salinity station 12 and low salinity station 5 in Table 8 shows that the low salinity station on August 11 had a greater number of survivals and new attachments than the high salinity station except for older sets of *B. glandula* in the third meter, and the new sets of *B. cariosus* in the second meter.

Two-thirds of the young at station 12 were attaching to rock surfaces while three-fourths of those at station 5 were attaching to mature barnacles often piling up to a depth of 15 cm, with the exception of the third meter level; there they did set on bare rock, crowding together making a solid mass 10 to 30 mm high. The moisture-holding and shade-producing properties of the very rough surface account for the different survival of the younger sets during the warm months.

c. *Miscellaneous Observations*

Observations made in 1930 on two low salinity stations, Barnacle Rock (station 5) and Parker Reef (station 3) showed that great changes had taken place since 1928 (Table 9). Great numbers of the old barnacles were dead and had been washed off. Young were abundant but their survival poor

except on the few remaining old barnacles. *C. dalli* was very abundant in all open spaces in the first and second meters.

TABLE 9. Comparison of total population changes per m² in two low salinity stations between 1928 and 1930: Barnacle Rock, station 5; and Parker reef, station 3.

Year	Meter level	Station 5			Station 3		
		Mature	Young	Total	Mature	Young	Total
1928	1	24,000	9,000	33,000	30,000	11,000	41,000
1928	2	29,000	4,000	33,000	28,000	8,000	36,000
1930	1	9,700	85,000	94,700	5,000	10,000	15,000
1930	2	11,000	59,000	70,800	1,000	7,500	8,500

Such fluctuations in the population of old and young barnacles indicates the importance of annuation in the composition of the community at any one time. A year in which tidal conditions favorable for the attachment of larvae are accompanied and followed by favorable conditions, meteorologic and otherwise, for survival and growth, brings about an increase in the one or more species favored. The large population persists for a period corresponding to the length of the life cycle of the species concerned (perhaps two years) unless in the meantime conditions become especially favorable for barnacle predators. Since especially favorable years may be separated by considerable intervals intermediate periods of small population intervene. Thus in 1928 and the year or years immediately preceding conditions seem to have been especially unfavorable for *Chthamalus dalli* in the areas investigated while conditions in 1929 or early 1930 favored the propagation of this species to the extent that it occupied all areas in which it did not compete at a disadvantage with the already established *B. glandula* and *B. cariosus.*

All shores visited in the region of Bellingham Bay and Samish Flats (stations 21 and 20) showed a heavy attachment of young and old barnacles of all three species through all three levels. The young, 2 to 10 mm in diameter, were mostly attached to the old, often piled up to a depth of 8 to 15 cm.

Apparently, from general observations, conditions were very favorable for seeding throughout the low salinity area during the latter part of June and the first week of July. Those that were fortunate enough to attach to old specimens dead or alive, had a high rate of survival. If there was heavy seeding during the middle part of July the greater portion died. There was a heavy attachment during the first and second weeks of August and few were dead when observed on August 8 and 9.

3. CONCLUSION

The arrangement of the various dominant species of barnacles at any time is the result of attachment, survival of young and death from age. The

series of events and the changes produced by them are significant when the detailed history is known in full. *Without* the entire series of environmental and biological events, local and irregular arrangements often found, can have no significance. This principle must apply to the details of plant arrangement in terrestrial communities and with special force to annuals and biennials.

Rasmussen made observation on this community at La Jolla, near San Diego, California, and his observations were confirmed by observations of the writer at Laguna beach, fifty miles farther north.

B. SOUTHERN CALIFORNIA BALANUS-LITTORINA COMMUNITIES

EFFECTS OF WAVE ACTION AND FRIABLE MATERIAL

D. I. RASMUSSEN

The tidal communities of the Pacific coast have been studied in considerable detail in the vicinity of the Puget Sound Biological Station and the papers of Shelford and Towler ('25), Towler ('30), Worley ('30), and Rice (30) indicate something of the composition and extent of these communities in that region. No corresponding studies have been published on other portions of the Pacific coast, although Shelford ('30) published the results of general observations which he made on the tidal communities from Alaska to Southern California.

The writer spent six weeks during the early part of 1931 in a study of the tidal communities of the southern coast region of California. All areas of rocky shores from Oceanside to San Diego Bay were visited and conditions noted. The most intensive work was done at Alligator Head, La Jolla, Mussel Rocks near Del Mar, and a rocky area along the northern portion of the Scripps Institution grounds. Vertical distribution was best shown on the concrete pilings at the Scripps Institution pier. The areas of shore line within the Institution's grounds provided exceptional advantages, as they have been closed to the collection and removal of any of the animals by the public.

1. GENERAL CONDITIONS

The whole area was not exceptionally rich in rocky shores. The coast line was along the face of eroding cliffs in many places and where rocks were present they appeared to be of a very friable nature which offered a poor foothold for sessile animals. No definite sheltered rocky areas were seen, the coast as a whole being rather uniform and all rocky shores subject to direct wave action. In most localities there was considerable sand present and in movement with the wave action.

Daily records kept at the Institutional pier and supplied me by Dr. Moberg

show an average salinity for January, February and March of 1931 as 33.78 gm of salt per 1 with extremes for the same period of 33.86 to 33.62 gm per 1, determinations made by the chlorine method. Average records for some years past show this to be slightly high, differing less than 0.1 gm per 1, however.

The range of the tides at La Jolla is not as great as that in the Puget Sound region, where most of the work on tidal communities has been done. This difference should be borne in mind in any comparisons.

The mean range of tides at La Jolla is 1.13 m and the extreme range above mean low tide, 1.55 m; at Cattle Point, San Juan Island, the mean range is 1.53 m, and the extreme range above mean low tide, 2.53 m.

This difference of three feet in the diurnal range of the tides means that on similar shores there would be over 50 per cent more area in the intertidal area on the San Juan Island shore than at La Jolla.

2. QUANTITATIVE OBSERVATIONS

Numerous area counts were made of the more abundant sessile animals. In making the counts a frame of 0.10 m² subdivided into squares measuring 0.005 m² was used. Counts were usually made on areas of 0.25 m² but for the smallest of the animals only 0.01 m² was used. Counts were made with the idea of covering typical groupings. The usual situation seemed to show two minor communities, appearing as parallel belts along the shore line. In numerous situations the seemingly characteristic animals of these communities were found intermingled with one another. Some species ranged over the entire intertidal area and so the two communities were not entirely distinct. Together they are considered as the Balanus-californianus association. The two modified communities within the associations are here designated as faciations.

The Mytilus-californianus Faciation,—From the lower low tide mean (0 tide) to a height of approximately 1.2 m, on the piling under the pier, was a nearly solid stand of the mussel *Mytilus californianus* Conrad. The mussel appeared as a true dominant, occupying the available surface. The barnacles, limpets, sea anemones and chitons were found living on the shells of the mussel, the crab *Hemigrapsus nudus* (Dana) and a number of small crustaceans in the spaces among the sessile forms. This is perhaps the ideal condition and ideal arrangement. A number of areas of abrupt and durable rocky shores showed the same condition in a lesser degree.

As judged from a variety of situations, the order of attachment on a bare surface appeared to be first the abundant barnacles of the acorn type. These did not necessarily precede the mussels, as mussels were seen establishing themselves on certain surfaces that were practically free from barnacles. The mussels establish themselves on all favorable situations, and many times at

the expense of other animals. There is no order in this replacement that can be interpreted as 'succession.' There were often situations where the starfish had eaten all the mussels from a small area, but other than that there seemed to be nothing that supplanted the mussels. The starfish only preyed upon them and did not take their place in an area.

Along the shore were numerous rocky places near the 0 tide mark in which mussels were not present, except in very small isolated groups. The friable rocks did not seem to afford the right kind of attachment, and other conditions were not ideal. In such situations the lowest part of the intertidal belt had quite a ground work made up of the native oysters, *Ostrea lurida* Carpenter, often covering the rocks completely. In areas near the oysters were the barnacles, *Balanus glandula* Darwin, and the thatched barnacles, *Tetraclita squamosa rubescens* Darwin attaining its maximum development. There were numerous chitons, limpets, small acorn barnacles *Chthamalus fissus* Darwin and the tube mollusk, *Aletes squamigerus* Carpenter. Small compact groups of the goose neck barnacle, *Mitella polymerus* (Sowerby) occurred where wave action was direct, but exposure to the sun slight. The subtidal barnacle *Balanus tintinnabulum californicus* Pilsbry extends upward for 0.5 meter from the subtidal area, in areas that are washed by waves at 0 or minus tides.

Littorina planaxis Faciation,—This is above the community described, that is, reaching from near the mid-tide line to well above mean high tide line, the usual groupings of animals consist of the acorn barnacles as the most conspicuous components. The most abundant species is the very small *Chthamalus fissus* Darwin, often making pure stands, one example showing 524 individuals on 0.01 m^2 or 52,400 per m^2. The usual arrangement on top of the rocks and on exposed surfaces was a stand of the two barnacles *C. fissus* and *Balanus glandula* Darwin at a usual ratio of fifteen to twenty Chthamalus to one Balanus. A single *B. glandula* occupies the equivalent area covered by five to seven *C. fissus*. Shelford ('30) gives the names of *Balanus hesperius* Pilsbry and *B. cariosus* (Pallas) as animals of the intertidal area at La Jolla. There is no doubt some mistake in the locality from which the specimens were taken, as both these species are northern in their distribution and do not extend this far south. (See Pilsbry, '16).

With the two barnacles and also well above high tide line were found the gray littorine, *Littorina planaxis* Philippi. This was very characteristic of the upper portion of the intertidal belt; it was most abundant in rock pockets but not confined to such situations. Numerous limpets, the principal one being *Acmaea persona* Eschscholtz, and the large owl shell, *Lottia gigantea* Gray, were also present, the latter not in any great numbers, but its large size and fairly uniform distribution made it conspicuous. The sea anemone, *Cribrina xanthogrammica* (Brandt) was abundant in the upper community,

but it occurred more often in mats on protected sides of rocks and in the tide pools. As many as 96 were counted in a pure stand on 0.025 m^2 which would equal 3840 per m^2; with this number they formed a complete covering. Their abundant occurrence in many places appeared to be aided by their ability to endure sand in the surf.

3. DISTRIBUTION OF TIDAL DOMINANTS

Numerous counts and studies were made of the animals on the concrete piling under Scripps Institution pier. Animals here showed a greater uniformity than in many other localities, which were seriously interfered with by man and other agencies. The animal population on the pier piling having been protected from disturbance was in many respects nearer that of a natural area than any area along the nearby coast. The greater number and compact arrangement of animals on the piling as compared with adjacent shore, is due no doubt to the more favorable conditions for obtaining food and the comparative freedom from any action by moving sand. The effect of the sand was plainly visible at the base of the individual pilings, both those subject to exposure in an average tide and a very low tide. Table 10 shows the

TABLE 10. Showing the total population of the tidal area based on counts of 0.025 m^2 at 0.166 meter vertical intervals from mean low tide to the upper limits of animals with reading at the maximum (2.1 m) and minimum (minus forty-three hundredths meter) [-.43m] tidal levels of 1931.

Tide range Feet and Meters	*Littorina planaxis*	*Chthamalus fissus*	*Acmaea persona*	*Balanus glandula*	*Lottia gigantea*	*Mitella polymerus*	*Mytilus californianus*	*Cribrina xanthogrammica*	*Balanus tintinnabulum californicus*	Total animals per 0.025 m^2	Total animals per m^2
7.0′=2.1m	0	0	......	......	......	......	......	......	......	0	0
2.0m—	2	80	0	......	......	......	......	......	......	82	3,280
	2	170	2	......	......	......	......	......	......	174	6,960
Mean high	5	338	6	5	0	......	......	......	......	354	14,160
5.3′=1.6m	3	270	6	26	1	0	0	......	......	306	12,240
	0	219	5	18	1	17	35	......	......	295	11,800
	......	97	7	9	0	53	14	......	......	180	7,200
1m—	......	67	4	11	......	66	7	0	......	155	6,200
	......	138	9	14	......	26	15	1	......	203	8,120
	......	126	2	20	......	18	14	3	0	183	7,320
	......	118	1	13	......	0	16	4	5	157	6,280
	......	123	1	3	......	......	19	3	8	157	6,280
0 tide	......	114	1	1	......	......	17	11	11	145	5,800
(Mean lower low)	......	x	0	0	......	......	x	x	x	x	x
Min. 1931	......	0	......	......	......	......	0	x	x	x	x
Minus 1.4′= .43m	......	......	......	......	......	......	......	x	x	x	x

vertical distribution on squares covering 0.025 m^2 = 6.22 inches on a side. All numbers on the same level across the table occurred in the same square. The vertical columns are for individual species, showing number per 0.025 m^2.

Several counts were made, but this appeared to be nearest average. It is not an average of a number of counts, but a typical count.

The value of this count is enhanced by the fact that the piling has been undisturbed by collecting since its establishment—the mussels here had attained a large size and apparently dominated the area where they were present. All other stands of mussels had been disturbed by bait collectors, etc.

C. Coactions, Reactions and Community Development and Extent

V. E. Shelford

There is undoubtedly competition for space. The chief coactions which are well known are the destruction of barnacles by the snail, *Thais,* and the starfish, *Pisaster.* Much of the feeding is done at high tide. Starfishes and Thais devour barnacles, and mussels are in competition with barnacles for space, but we have seen no evidence that the tidal species are limited downward by predators. The physical factors appear to be the principal control.

Aside from covering the surface with shells there is little reaction on the substratum. Rice, however, found that barnacles attached much better to rock that had been submerged with every tide for a long period than to rocks moved into the intertidal areas from land. This suggests succession.

Miss C. J. Kelley determined the age of several sets of piling in the Balanus-Mytilus edulis area and found that the three principal dominants, *Mytilus edulis, Balanus cariosus,* and *Balanus glandula,* were all present on the piles six months old. Piles one year old merely showed more and larger specimens of the same species. This confirms the findings of Pierron and Huang ('26) and supports the view that there is development without succession in tidal communities (Brandt, '96). Development is also of a short duration.

The life histories of tidal animals are not well known. The life span of barnacles is supposed to be two years. Except for *Mytilus edulis* (Mossop, '22) which reaches six years, other species have not been investigated. Experiments having to do with survival of important species under adverse conditions were referred to under the discussion of the subtidal community.

This community occupies an area bounded roughly at its lower limit by the mean of one-half the lowest tides in each month and at its upper limit by the high tides. It is therefore from two to four meters wide, vertically, but essentially thousands of miles in length. Studies by Newcombe ('35), Appellof ('12), and others indicate similar communities in the north Atlantic

which leads to the suggestion that but one type of tidal community divisible into two or more biomes occupies the northern hemisphere, north to the ice-bound shores. *Mytilus edulis* is the only important dominant common to both the Atlantic and Pacific. The work of Oliver ('23) shows a complete change of dominant species as well as many of the dominant genera in the southern hemisphere about New Zealand. The difference in taxonomic composition between this community and sub-tidal communities is usually sharp. *Balanus cariosus* and *glandula* cease to be present in a sharp line as do all other important species. Subtidal barnacles are fully as definitely distributed and do not (ordinarily) overlap appreciably. Rasmussen found a subtidal barnacle slightly overlapping the tidal species. Gislen ('31) indicates a similar possibility on the Swedish coast.

II. Pandora-Yoldia, Strongylocentrotus-Argobuccinum and Macoma-Paphia Biomes

V. E. Shelford

A. Comparisons

Comparing the Strongylocentrotus and Macoma communities, there is the greatest correspondence among the small animals of the plant layer-kelp *(Nereocystis luetkeana)* in one case and eel grass *(Zostera marina)* and allied species in the other. *Margarites succinctus, Lacuna porrecta*, and *Lacuna divaricata* are more abundant, and practically always present on the kelp. One or both of the latter two are often wanting on eel grass and their presence seems to depend upon the eel grass being near the kelp. It is perhaps also favorably influenced by the growth of brown algae on the eel grass. Caprella occurs in abundance on eel grass to which brown algae are attached. On the other hand, the large isopod *(Pentidotea)* is nearly always present on eel grass and almost as often on Nereocystis. On the bottom the ecotone between the two communities is a mere mixture of dominants, usually between 5 and 10m below low tide (Wismer and Swanson, p. 333).

As shown in Figs. 3, 4 and 7, there is a narrow belt of a faciation of the Strongylocentrotus-Argobuccinum biome just below the tidal community area or the Macoma-Paphia biome as the case may be. This is due to the better circulation and wave action that leaves coarse bottom materials exposed and bare.

1. motile animals

Some marine species, like birds and mammals on land, occur in two or more biomes or move from one to another from season to season. Similarly the marine mammals listed on page 263 and those forms listed below are widely distributed.

TABLE 11. Motile species found in more than one community.
A = abundant; C = common; F = few; X = present.

Biome names are indicated by initial letters:	S-A	P-Y	M-P
Liparis pulchellus Ayres	X	C	C
Lepidopsetta bilineata (Ayres)	X	C	C
Psettichthys melanostictus Girard	X	C	C
Pandalus goniurus Stimp.	F	A	
Spirontocaris gracilis (Stimp.)	F	C	X
S. tridens Rath.	X	X	
S. townsendi Rath.	X	X	
S. suckleyi (Stimp.)	F	F	
Crago alaskensis (Lock.)	C	A	X
C. nigricauda (Stimp.)	C	A	—
C. alaskensis elongata (Rath.)	C	A	—
C. dalli (Rath.)	X	C	

B. Seral Communities in East Sound in Relation to Physiographic Processes

A. O. Weese

1. Localities and Methods

During the summer of 1929 a general survey was made of the bottom fauna of East Sound and adjacent interior waters of the San Juan Island group. The data obtained have a bearing upon problems of marine succession and upon the interpretation of fossil remains. East Sound is a long, narrow, body of water extending into the south side of Orcas Island which surrounds it somewhat in the shape of a horse-shoe. The length is about 12 km and the average width about 1.8 km. The shore line is rugged except at two points, where the villages of Rosario and East Sound are located. The latter is at the head of the sound, which is here divided by a low, rocky headland into two shallow bays, Fishing Bay and Ship Bay. Of these the second is bounded by a sandy beach from which the landward slope is gradual to an altitude of perhaps fifteen meters, followed by a similar downward slope to sea level on the north side of the island at a distance of approximately 2 km. This is the lowest portion of the island and may represent a former strait. The depth of the sound, off shore, varies from twenty to thirty-five meters, but the greater part has a relatively uniform depth of about thirty meters. The bottom material ranges from a very heavy organic mud in Fishing Bay to a mud having a considerable admixture of sand and shell at the mouth.

The principal method of collection was the use of the Petersen bottom sampler, which brings up the surface mud of the sea bottom with the contained animals from an area of 0.1 m^2. The larger, less frequent animals are not accurately represented in the catch, nor are motile forms collected

with any degree of quantitative accuracy. The census of the smaller sessile and inactive forms may be considered, however, as reasonably accurate. In addition, a study of the beach fauna at the head of Ship Bay was made, measured areas being dug up to a depth of 20 cm. The location of the stations at which collections were made is indicated in Fig. 7, and further data are given in Table 12.

Stations 63 and 66 are located in more open waters communicating with the broad Rosario Strait by way of Obstruction and Peavine Passes and more indirectly by way of Thatcher Pass. In the opposite direction communication is with San Juan Channel by way of Upright Channel. Circulation is relatively unimpeded and the bottom material contains a much larger proportion of sand, gravel and shell than elsewhere within the area investigated. The community here may be considered as marking an ecotone between the Strongylocentrotus-Argobuccinum biome (Shelford and Towler, '25) of the regions above mentioned and the Pandora-Yoldia biome (see

TABLE 12. Data in regard to stations at which collections were made.

Station	Height above mean low tide	Character of bottom	Percentage of bottom material retained by 0.2mm. screen	Organic remains identified in bottom material	Remarks
113_1....	1.0m.	Sandy mud	...	....	
113_2....	0.3	Firm sandy mud	...	....	Matted *Enteromorpha*
	Depth below mean low tide				
113_3....	0.1	Sandy mud	...	....	In patch of Zostera
74	20–25	Soft mud	3%	*Coscinodiscus* sp. Foraminifera	Strong odor of H_2S No sand
73	10	Sandy mud	2%	*Coscinodiscus* sp.	Larger particles mostly sand
73_2....	15–20	....	...	....	Not as much sand as 73 No. microscopic examination
72	30	Mud-soft	...	Chaetopterid tubes	No microscopic examination
72_2....	30	Mud—not so soft	...	....	"
71	26	Mud	8	*Coscinodiscus* sp.	
68	24–26	Mud and shell	1	*Coscinodiscus* sp. *Arachnoidiscus* sp. *Biddulphia* sp.	Small fragments Molluscan shells
65	28–30	Mud and shell	3	*Coscinodiscus* sp. *Arachnoidiscus* sp. *Biddulphia* sp. Chaetopterid tubes	Shell fragments larger than in 68
66	24	Mud, shell, gravel	...	Chaetopterid tubes	No microscopic examination
64	36	Mud, sand	32	*Coscinodiscus* sp. *Arachnoidiscus* sp.	Larger particles Mostly sand
63	50	Gravel, mud, shell	...	....	No microscopic examination

Shelford, p. 269) of East Sound. The present paper is concerned chiefly with the phenomena of succession in the latter.

The predominant physiographic processes seem to tend toward land formation at the head of the sound, so that stages of a landward sere may be observed northward from the mouth. Within the sound, deposition of silt is taking place at a rapid rate (see Shelford, p. 266). Quartz sand makes up a considerable portion of the deposit near the mouth of the sound and also, locally (Ship Bay), at the head; molluscan shells also play an appreciable rôle, especially in the outer part, but everywhere organic debris is the most important constituent of the bottom material. Intact shells of larger diatoms may make up as much as 10% of the upper layer.

2. COMMUNITIES

Census data for each station are given in Table 13, and the relative abundance of the more important dominants in the bottom collections is shown graphically in Fig. 8. Two biomes are represented: 1. The Macoma-Paphia biome; and, 2. The Pandora-Yoldia biome, the latter showing several well defined faciations.[12]

A. *Macoma-Paphia Biome*

The Macoma-Paphia community is characterized by the usual dominants of the Macoma-Paphia association. All the more important dominants are listed in Table 13. Shelford, see page 276, has pointed out that there are many faciations of this community. This one is characterized by *Notomastus pallidior* Chamb. Approximately 5000 annelids of this species occurred per square meter at a level 1.15 m above mean low tide. Shelford did not study the Macoma-Paphia biome in detail, and the annelids of Wismer and Swanson (page 341) were lost enroute to identification which renders comparison difficult. However, the presence of such great numbers of annelids is unusual.

B. *Pandora-Yoldia Biome*

This community has been described by Shelford (see page 266). Most of his studies were made in the area 63, 64, 65, 67, 68, 69 and subordinate stations south of 68. He has characterized the community of this area as the Cucumaria-Scalibregma association. Important species found throughout the area studied (Fig. 8) are *Scalibregma inflatum* Rathke, *Paraprionospio tribranchiata* Berk., and *Macoma brota* Dall. The last named species was represented in the collections by immature individuals only, and is probably an annual. Absent only in the extremely dense mud of Fishing Bay are *Phacoides tenuisculptus* Carp., *Glycinde armigera* Moore, *Amphicteis glabra* Moore, and

[12] Mollander ('30) has used *facies* for the variation of an association characterized by the addition of a species and Clements ('26) has used the same root in *faciation* to indicate the addition or loss of an important species; e.g., Cucumaria-Scalibregma Association—Cucumaria-Scalibregma-Ammochares Faciation.

the Ophiurid *Amphiodia occidentalis* (Lyman). Shelford found this species in large numbers in 1926, but not in 1930. There is evidently a great variation in abundance from year to year. Among the above species are to be found the binding dominants of the association and the various faciations characterizing the area here considered.

(1) Typical Cucumaria-Scalibregma Association.

Stations 64, 65, and 68 may be considered as representing the typical Cucumaria-Scalibregma association. *Cucumaria populifera* (Stimp.) was present in enormous numbers at 64 and 65. However, the individuals collected were mostly juveniles and seemingly represented the results of especially favorable conditions for reproduction. Other important dominants are *Pandora filosa* Carp., *Sternaspis fossor* Stimp., *Phacoides tenuisculptus* Carp. and *Dentalium rectus* Carp.

(2) Diopatra-Chelysoma Ecotone.

Stations 63 and 66, as mentioned above, may be considered as representing an ecotone (Diopatra-Chelysoma ecotone, Shelford (page 269) between the Cucumaria-Scalibregma association and the Strongylocentrotus-Argobuccinum biome. While most of the species found in the typical Cucumaria-Scalibregma association are found also in the ecotone, populations are much reduced and the number of additional species is very large.

(3) Scalibregma-C. piperata Faciation.

Indicated on the map (Fig. 7) in shallow water between the Cucumaria-Scalibregma association and low tide line is a narrow belt in which *Cucumaria piperata* (Stimp.) replaces *Cucumaria populifera*. This faciation is included on the basis of data furnished by Shelford.

(4) Heteromastus filibranchus Faciation.

Beginning with Station 71, there is a progressive dropping out, first of Cucumaria and Dentalium, then of Pandora, Yoldia, *Lumbrinereis bifurcata* McInt., *Natica aleutica* Dall, and others. New species coming in are the annelids *Heteromastus filibranchus* Berk., *Spiophanes cirrata* Sars, and *Spionides japonicus* Moore. This faciation is characterized by the progressive loss of species as one goes up the Sound and an increase in annelid population. *Scalibregma inflatum* is very abundant. *Heteromastus filibranchus* is chosen as the characteristic added species.

(5) Ammochares-Euclymene Faciation.

The annelids mentioned as new dominants in the preceding faciation drop out entirely in the shallower waters of Station 73, and give way to a new group, *Ammochares fusiformis* (Delle Chiaje), *Pista cristata* Muller, *Lumbrinereis latreilli* Aud. and M.E., *Euclymene* (*reticulata*? Moore) and others. The last named species appeared first at Station 73_2. The others occurred

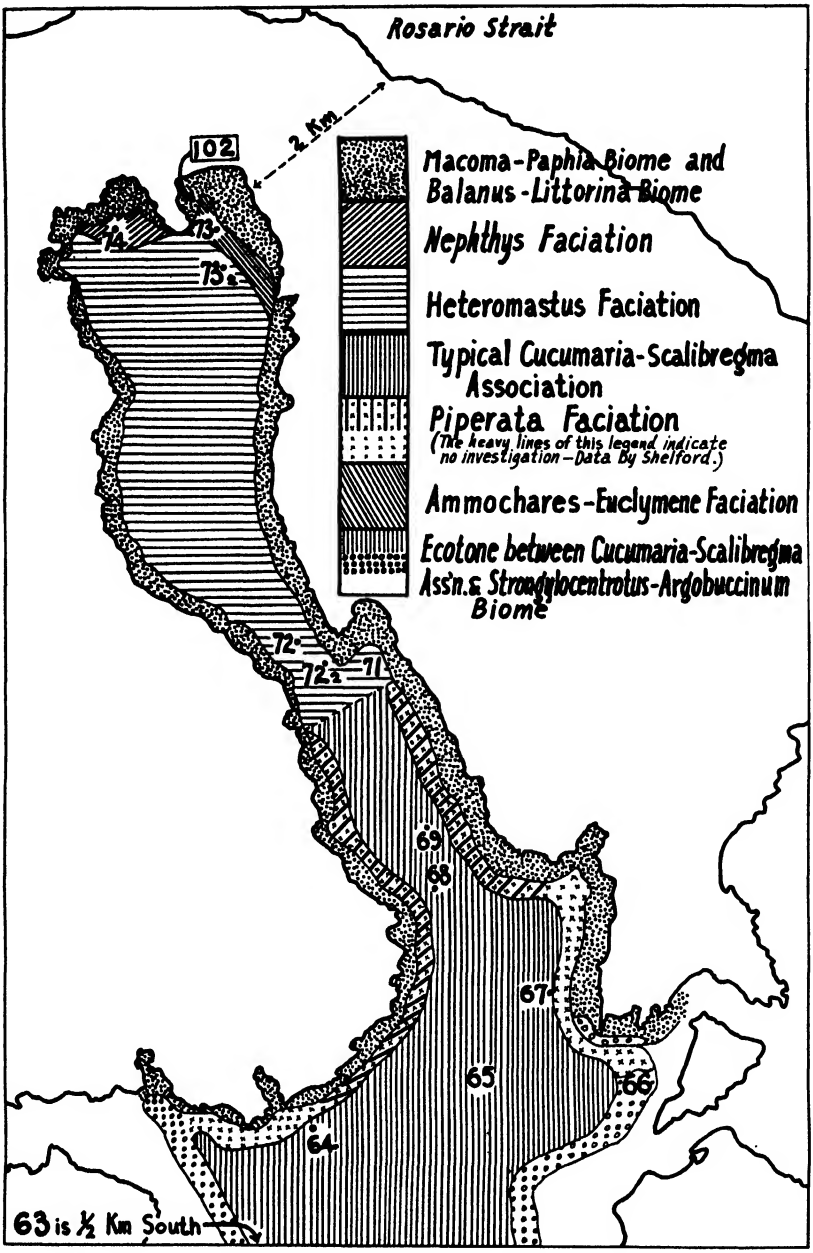

FIG. 7. Provisional map indicating the faciations of the Cucumaria-Scalibregma association (Pandora-Yoldia biome) in and adjacent to East Sound. Either a narrow strip of Macoma-Paphia biome, or the Pisaster ochraceus faciation of the Strongylocentrotus biome occurs between the Cucumaria-Scalibregma association (or its faciations) and mean low tide. The width of both of these is greatly exaggerated. The intertidal area is occupied locally by the Macoma-Paphia biome in its lower edge and by the Balanus-Littorina biome elsewhere. These details cannot be shown, to scale, on this map.

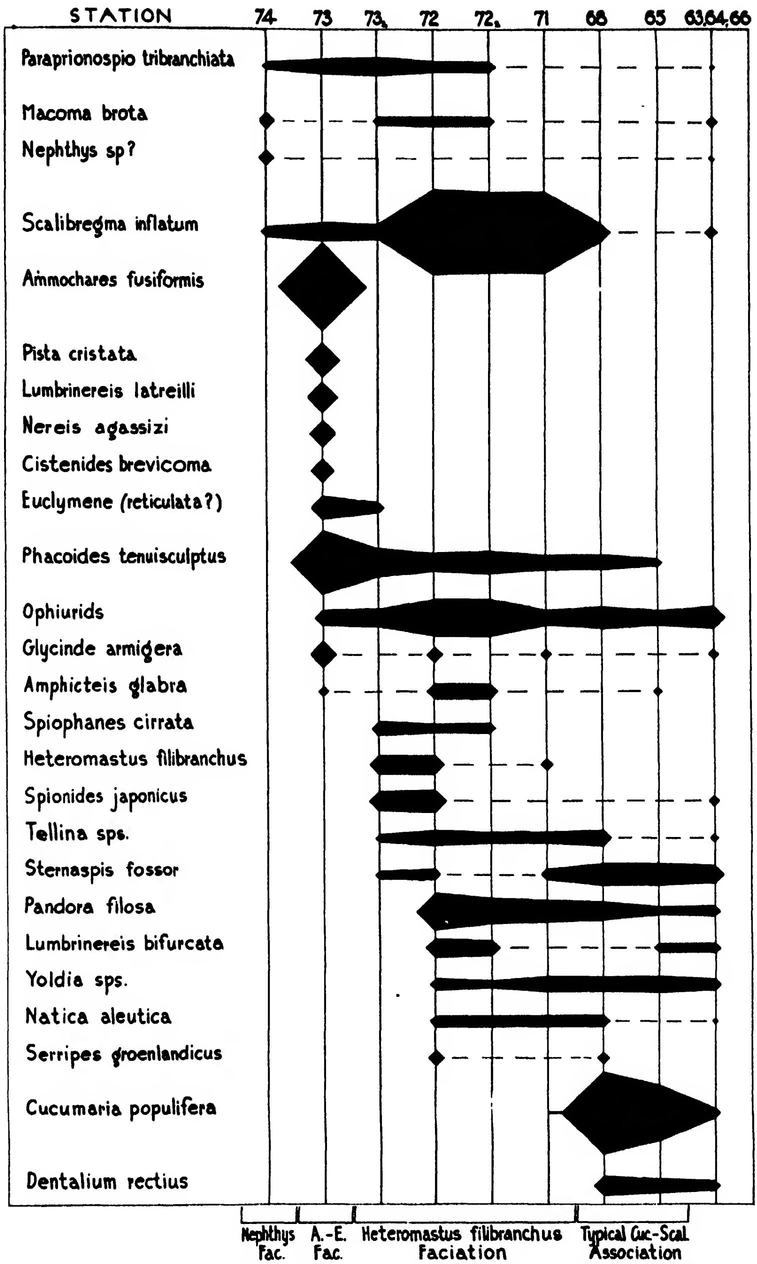

FIG. 8. Showing the distribution of important dominants in the area studied. In order to space the Lohmann[18] spherical type curve in which the width of a black line on the ordinate of a given station is proportional to the cube root of the population at that point. The species here represented are indicated by asterisks in Table 13, where actual populations are given. A. — E. =Ammochares-Euclymene.

[18] Wissensch. Meeresuntersuch. K. Kom., Abt. Kiel, 10:192-194, 1908.

only at Station 73. The area occupied by this community is evidently small and it might accordingly be referred to as a lociation (see Shelford, page 292). The total population here was the largest recorded except that of the upper beach station and the number of species of annelids was largest. The total number of species present was exceeded only at Station 72 and the ecotone stations. *Phacoides tenuisculptus* is also present here in maximum numbers.

Table 13.

Table 13. Showing the distribution of species and their abundance in the area of study. The table is broken into sections to indicate the natural communities into which the population falls. The figures indicate population per square meter. Asterisks indicate species whose population is represented in Figure 8.

	113$_1$	113$_2$	113$_3$	74	73	73$_2$	72	72$_2$	71	68	65	63,64,66
Approximate depth in m below MLT	+1.15	+.5	0.1	22	10	15–20	30	30	26	25	29	24–50
Notomastus pallidior Chamb.	5000	4										
Macoma nasuta Con.	150	92	50									
Macoma inquinata Desh.	24	24	22									
Macoma secta Con.	30	2										
Paphia staminea Con.	14	30	20									
Cardium corbis Mart.	10	8	4									
Nephthys caeca Fab.	8	22								2		1
Nephthys hombergii Aud. & M.-E.			2								3	1
Schizothaerus nuttalli Con.		26										
Cardium californiense Desh.		8										
Saxodomus giganteus Desh.		6										
**Macoma brota* Dall				8		1	2	2				2
**Nephthys* sp.				8							1	
**Paraprionospio tribranchiata* Berk.				1	8	17	4	4				x
**Scalibregma inflatum* Rathke				2	16	7	1565	1360	1278	15		3
**Ammochares fusiformis* (Delle Chiaje)					1692							
**Phacoides tenuisculptus* Carp.	6				616	57	14	27	8	6	1	
**Pista cristata* Muller					100							
**Nereis agassizi* (Ehlers)					36							2
**Euclymene* (*reticulata* Moore?)					34	5						
**Cistenides brevicoma* (Johns.)					24							
Scoloplos elongata Johns.					18	1						1
**Glycinde armigera* Moore					39		6		2			2
**Lumbrinereis latreilli* Aud. & M.-E.					62							
Lumbrinereis impatiens Clap.							1					x
Nereis procera Ehlers					8							
Glycera rugosa Johns.					5		1					
Pectinaria auricoma (Muller)					4	1						
Ammotrypane sp.?					2							
Glycera tesselata Grube					2							
Phyllodoce sp?					2							
Maldanid					2				2		1	x
*Ophiurids					8	12	143	108	10	25	11	24
**Amphicteis glabra* Moore					2		10	4			1	

(6) Nephthys Faciation.

At Station 74 the population is reduced to a minimum, the only species remaining being *Scalibregma inflatum, Macoma brota, Paraprionospio tribranchiata,* and an undetermined species of Nephthys. Other undetermined specimens of this genus were taken at Stations 64 and 65 but the species is probably not the same. The lack of an accurate determination of this species makes its use in nomenclature of somewhat doubtful propriety, but this community may be called, tentatively, a Nephthys Faciation.

	113_1	113_2	113_3	74	73	73_2	72	72_2	71	68	65	63,64,66
Approximate depth in m below MLT	+1.15	+.5	0.1	22	10	15–20	30	30	26	25	29	24–50
**Heteromastus filibranchus* Berk.						14	12		4			
**Spionides japonicus* Moore						16	27					2
**Spiophanes cirrata* Sars						8	2	2				
Nereis notomacula Tread.						x						x
Anaitides mucosa Oersted						x						x
Streblosoma bairdi (Malm.)						x						
**Tellina* sps.						1	6	4	4	10		1
**Pandora filosa* Carp.							116	50	24	18	1	2
**Lumbrinereis bifurcata* McInt.							18	6			2	2
**Yoldia* sps.							5	1	6	8	9	4
Psephidia sps.							8			2		x
Lyonsia californica Con.							7					
**Serripes groenlandicus* Gmel.							7			2		
Marcia subdiaphana Carp.							4	2				
Glycera capitata Oersted							3				2	
**Natica aleutica* Dall							3	4	4	4		x
Glycinde sp?							1					x
Ampharete gracilis Malm.							1					
Ampharete arctica Malm.							1					x
Goniada brunnea Tread.							1					
Pilargis berkeleyi Monro**							1					
Glycinde sp?							1					x
Leodicid sp?							1					
Lumbrinereis sp?								10				
Glycera nana Johns.								2				
Leptosynapta sp?							1			21		4
**Sternaspis fossor* Stimp.						1	3		4	26	21	20
**Cucumaria populifera* (Stimp.)										1295	460	2
**Dentalium rectius* Carp.										12	10	4
Capitellid sp?										2		
Nephthys cirrosa Ehlers											2	
Sabellid sp?											1	
Polynoid sp?											1	x
Lima sp?											1	
Total population per M^2†	5276	266	104	19	2683	205	1993	1612	1368	1454	562	132
Total Species	15	19	8	4	26	29	39	23	19	20	23	62
Population annelids per M^2	5016	36	6	11	2058	84	1659	1391	1294	45	35	39
Species annelids	5	5	3	3	20	15	19	9	7	4	10	16

**Ann. and Mag. Nat. Hist., 11:673-675. 1933. †Some species not recorded.

3. SUCCESSION

Conditions in East Sound suggest the following successional relationships following the closing of the sound.

If East Sound were at one time a strait it would have been characterized by a Strongylocentrotus-Argobuccinum fauna now typical of large areas of more open waters (Strongylocentrotus-Argobuccinum biome). Important dominants would have been *Strongylocentrotus drobachiensis* Moel., *Argobuccinum oregonensis* Red., *Balanus nubilis* Dar., etc.

A. With the partial closing of the present head of the Sound would have come, with the deposition of organic debris, a transition by way of a Diopatra-Chelysoma ecotone condition to a Pandora-Yoldia fauna.

B. The latter stages of the process after the closing of the head of the Sound involving the progressive deposition of organic debris are evident in the present condition of the area. The typical Cucumaria-Scalibregma association is giving way to the Macoma-Paphia biome through a series of faciations described in this paper, involving a gradual loss of species and an increasing dominance on the part of *Scalibregma inflatum* and other annelids (Heteromastus faciation).

C. Where considerable amounts of inorganic material are added to the bottom material by the outwash of littoral sand the transition to the Macoma-Paphia biome is by way of a faciation involving increased dominance on the part of *Phacoides tenuisculptus* and the appearance of a different group of annelids (Ammochares-Euclymene Faciation).

D. With increased deposition of organic debris without the addition of sand, resulting in a soft organic mud with a high H_2S content, the fauna becomes extremely depauperate, and, as a part of the sere leading toward a mudflat, we have a community which we have designated as a *Nephthys Faciation.*

4. INTERPRETATION OF FOSSIL DEPOSITS

In favorable localities where bottom materials have not been worked over by wave and current, we should be able to identify successive layers of deposits containing fossil remains of animals representing the communities above named. Stage 1 should be easy of identification with its large number of shell-bearing dominants. Stage 2 would be characterized by the dropping out of such forms as Argobuccinum and Balanus, an increase in organic debris evidenced chiefly by the presence of shells of diatoms, and the appearance of Pandora, Yoldia, Phacoides, etc. The disappearance of these molluscs in turn, with a corresponding change in the character of the soil would indicate the later faciations. It is to be hoped that investigations of this type may be undertaken in the East Sound area. The application of similar methods to the study of fossil deposits elsewhere might be expected to yield results worthy of consideration.

C. EARLY STAGES OF SUCCESSION FROM MARINE CONDITIONS TO LAND

ARCHIE MACLEAN

The area of study includes a small inner lagoon nearly cut off from the larger bay by a gravel bar. This lagoon was almost filled with mud, etc. It may, however, be assumed that this at one time was similar to a small lagoon southeast of Friday Harbor (Newhall's Lagoon) which was a typical Cymatogaster-Haminoea community (see Powers, '20, p. 379; Muencher, 15, Fig. 10, unnumbered lagoon now destroyed by a park development). It did not drain entirely at low tide and had a mud bottom. Newhall's Lagoon, the one studied by the writer and a later stage (station 101) briefly described by H. C. Markus (page 324), constitute a series in which biotic factors dominate in succession.

From the studies of Weese it is made evident that with changes in topography, the change from sea to land communities is initiated in a Macoma-Paphia community. The locality which forms the basis of this paper presented a series of stages different from these described for Fisherman's Bay by Shelford and Towler ('25). It indicates, as has already been pointed out on page 279, that there are probably various successional routes from marine to terrestrial communities. The purpose of this study was to determine the changes in community composition which accompany deposition in nearly enclosed arms of the sea where the growth of saline plants and finally other land plants is beginning in the older portions.

1. LOCATION AND METHODS

The observations were made in August, 1930. The place chosen for this study was the inner end of Wescott Bay, near Roche Harbor, San Juan Island, Washington, termed locally Wescott Creek (Fig. 9). It is almost enclosed and an unusually protected body of salt water. The bay extends inward from the northwest side of San Juan Island for over a mile. Its entrance is very narrow and is also protected by Henry Island. The bay is thus well protected and the inner end is not subject to severe wave action. A ridge of sand which has been thrown up, and on which *Salicornia* has gained a foothold, almost cut off the inner tidal lagoon. The lagoon behind this ridge is completely filled at high tide; at low tide the whole area is exposed. The water drains off through a depression in the ridge.

Substations were established at various levels in front of and behind the Salicornia covered ridge (Fig. 9). The first five substations were located in front of it at 3, 2.6, 2.43, 2.2., and 1.65 m below high tide. Substation 6 was in the run off channel at 1.49 m. Substation 7 was back of the ridge on the mud flat at 1.67 m. Substation 8 was located far back in the area near the land at 1.2 m below high tide.

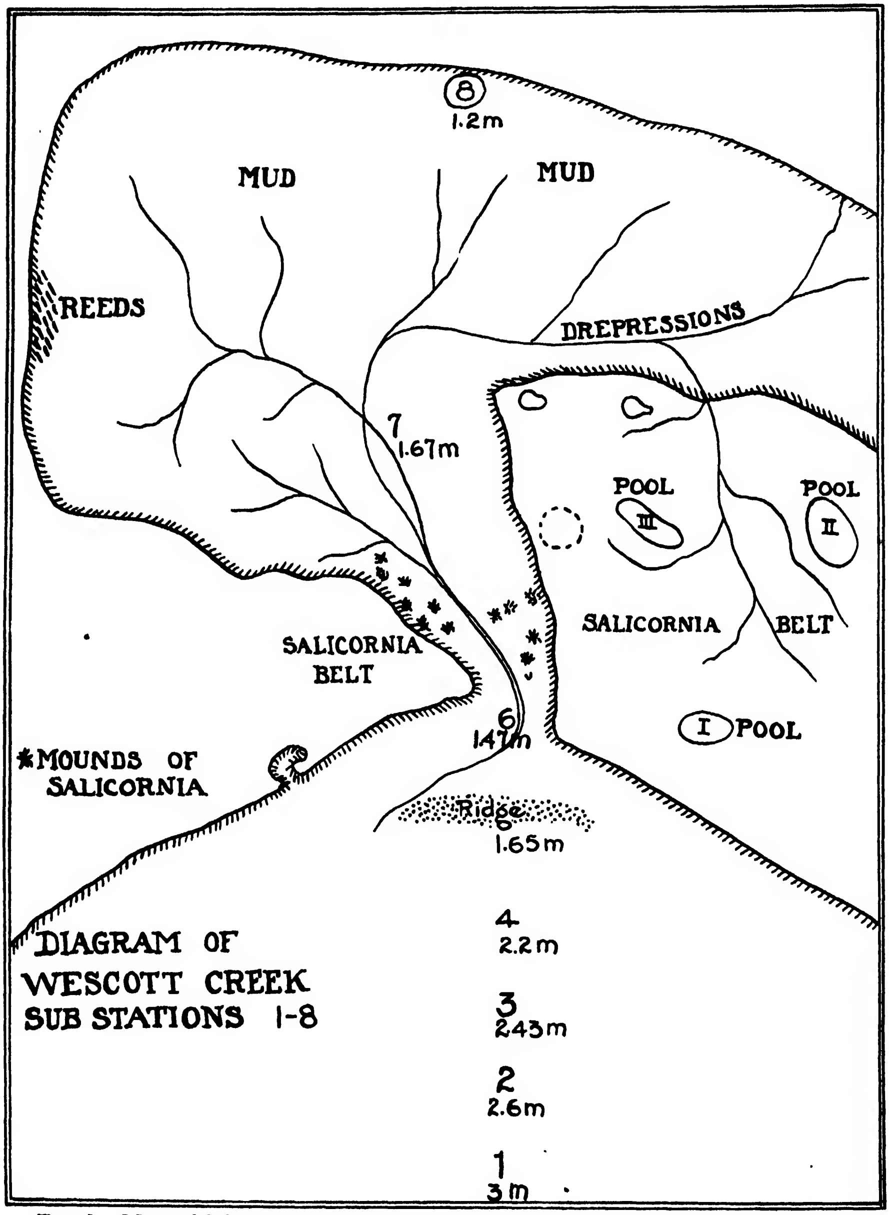

FIG. 9. Map of Wescott Creek (station 101), showing the distribution of study stations, pools, "run off" depressions, and the Salicornia beds.

In the large Salicornia belt were several pools and depressions which were once pools. Three of these, in various stages of evaporation were selected for study (Fig. 9).

Water samples were taken at each station. Three samples were taken on

different days and conditions of the tide. Those referred to in this paper were taken in the morning as the tide was going out. The alkalinity and salinity of the water was noted. The alkalinity was determined with standard acid and methyl orange and calculated as parts per million of calcium carbonate; salinity was determined by the silver chloride method.

Sand samples were collected according to Bruce's ('28) method, and titrated back with sodium thio-sulphate. The hydrogen sulphide was calculated as cubic centimeters per liter.

Two square meters were dug at each station. The sand was turned over with a shovel to the depth of two feet. The specimens obtained were listed for each station and are summarized in the accompanying chart, Fig. 10.

2. GENERAL CONDITIONS; TABLE 14

The alkalinity, in general, increases at each station up to the sixth, dropping to lower levels at the last two stations. The decrease in alkalinity at these stations may have been due to the entrance of fresh water by seepage.

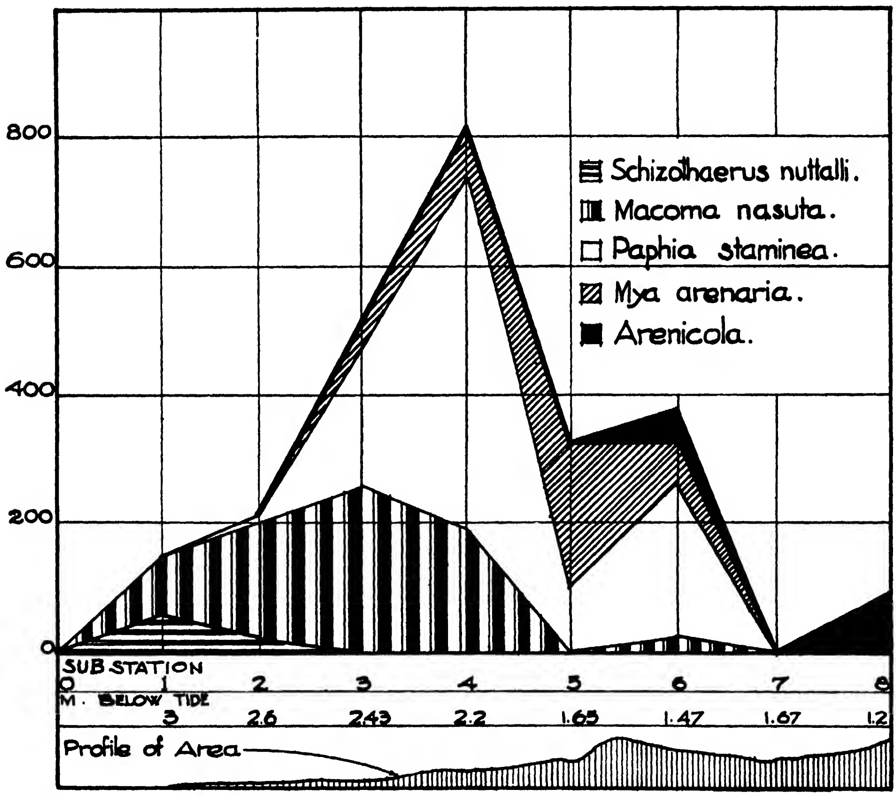

FIG. 10. Showing the distribution of the several important marine animals in the sere toward land.

These stations were nearest rapidly rising land. It will be noted that the alkalinity of the pools became low, decreasing as the water in the pools became less.

The salinity was about the same at each station but shows irregularities to be expected due to the differences in salinity of the different layers of water filling the pool at high tide. One of the three pools in the *Salicornia* belt, however, showed very high salinity as was to be expected.

These pools represented several different stages of depth and evaporation and showed one of the routes of succession to land.

TABLE 14. General conditions at Wescott creek, Station 101 (Substations 1-8 and I-III).

Substations	Meters	Alkalinity	Salinity gm./1	Hydrogen Sulphide cc/1
1	3m	104	29.26	1321
2	2.6m	80	28.51	887
3	2.43m	116	28.00	885
4	2.2m	110	26.61	1747
5	1.65m	130	27.33	2038
6	1.48m	186	29.26	1245
7	1.67m	138	27.55	1411
8	1.2m	114	29.26	1657
Pool I		126	32.48	....
Pool II		88	66.83	....
Pool III		62	25.82	....

The iodine absorption (calculated as hydrogen sulphide) of the mud was very large. It varied at the different stations depending upon the amount of decaying organic material present. At substation 5, which was just in front of a small sand ridge, there was a large amount (2038 cc per 1). Few animals were found here. Apparently large amounts of hydrogen sulphide and organic matter do not make for favorable living conditions for animals. Many dead shells were found at this station. Probably some unfavorable conditions arose which killed off the bivalves.

3. DISTRIBUTION OF ANIMALS

The abundance and distribution of the animals found are shown in Table 15 and Figs. 9 and 10. The last shows *Paphia staminea* to be the abundant bivalve. *Macoma nasuta* next in abundance. *Mya arenaria* is found at higher levels. It will be noted that bivalves were most abundant between 2.4 and 1.8 m below high tide. None were found at substations 7 and 8. Apparently the muddy area, poorly drained and with possible inward seepage of fresh water, is not a favorable environment for them. Most of the bivalves were found in decreasing numbers at the three meter level except *Schizothaerus nuttallii* which increased. S. nuttallii was not found above 2.4 m below high tide.

TABLE 15. Distribution of animals; number per 10 m².

Species	Substations							
	1	2	3	4	5	6	7	8
Macoma nasuta	110	180	270	200	0	20	0	0
Paphia staminea	0	30	260	500	100	250	0	0
Schizothaerus nuttallii	60	20	0	0	0	0	0	0
Arenicola sp.	0	0	10	10	10	60	10	100

Specimens of *Mytilus edulis* were found in a few places attached to logs, bearing barnacles. They were of typical shape for this species and fairly large. No small or young ones were found.

Flat muddy areas usually yield an abundance of worms. With the exception of Arenicola, worms were here present in insignificant numbers. Arenicola was found at each of the higher levels back through the mud area.

In the pools scattered over the mud area, the small goby, *Clevelandia ios*, was quite abundant. On top of the mud many small diptera were found, in some areas more than others, twenty per square meter being counted near substation 7.

From all observations, succession to land is taking place here. Physiographic forces are at work. A ridge of gravel has been thrown up across the end of the tide lagoon (Fig. 9). A small new ridge is now being thrown up across the opening. The lack of wave action allows the mud and debris deposited to remain without being disturbed. The water continuing to flow slowly from the back area with each high tide has kept a depression open. As the large ridge remained above the high tide Salicornia gained a foothold, grew and held the sand. Tufts of Salicornia are now appearing on raised portions of the back area. The pools which remain in the Salicornia belt are becoming smaller and drying up.

Pool I contained about two feet of water. It was almost circular and about three feet in diameter. The sides were straight with Salicornia growing up to the edge. Green algae covered the top of the pool. There were many mosquito larvae in the water. Pool II was of similar size. There was only two inches of water in the bottom. Dead Algae covered the bottom and no evidence of insect life was found. A week later this pool was dry. Pool III was larger than the others and was dry except for a small pocket of water near the edge. There were other depressions in which a growth of Salicornia covered the bottom.

The stages of animal succession seem to pass from the Macoma-Paphia association into an Arenicola consocies for at sub-stations 7 and 8 no bivalves were found. The worm, Arenicola, continued back through sub-station 8 which was just in front of the invading land. In this case the Macoma-Paphia association did not remain to the late stages toward land. The

Arenicola consocies gives way to the Salicornia in the lagoon proper and to reeds and tall plants about the edge.

A. In mud bottom portions of the area where there is poor drainage, no bivalves were found.

B. Bivalves are favored by or tolerate a certain amount of organic matter and sulphur compounds (measured in H_2S), but excessive amounts appear unfavorable to them.

C. Worms other than Arenicola were exceptionally few. Arenicola increased in numbers toward the shore. Thus, Arenicola is one of the last marine animals inhabiting the mud.

D. Succession to land proceeds by two routes within this small area: namely, through a Salicornia dominated community on high spots and a rush dominated community around the edges.

D. LATE STAGES OF SUCCESSION TO LAND

H. C. MARKUS

The relations of the Cymatogaster-Haminoea faciation to the invasions of Salicornia is not clear. However, it appears that this plant comes in on hummocks after other plants have dropped out.

A preliminary study of succession from Salicornia to climax forest was undertaken during the month of July, 1930. The observations were made at the inner end of a bay on the north shore of Shaw Island (station 110). A 2000 m^2 area of Salicornia appeared to be growing on a filled pool behind a gravel bar at the inner end of the bay. A small relic pool occurred near the center of the Salicornia area. On its landward side, Salicornia had been succeeded by grasses which covered a belt about four meters wide. Behind this was a forest edge of deciduous shrubs which was being invaded on its landward edge by conifer seedlings of the same species as the trees in the adjacent forest.

The snail *Syncera translucens* Carp. was exceptionally abundant in the Salicornia. Some leaf hoppers occurred but they were more abundant in the grass-covered area. The grasses supported grasshoppers and other insects and spiders. In the forest edge which was invading the grass-covered area, a great variety of land arthropods occurred, some belonging to the same species as the grass inhabitants. Snails and slugs were among the more representative invertebrates of the forest edge. It also presented the usual birds and insects characteristic of such areas in the region.

DISCUSSION

By

V. E. SHELFORD

I. COMPARISON WITH OTHER INVESTIGATIONS

Comparison with communities elsewhere is rendered difficult except in a few cases. The viewpoint and method are usually quite different from ours. In the case of the area exposed at the lowest tides, much work has been done, but usually with much confusion. Tidal and subtidal communities cannot be distinguished on a habitat basis, and have been treated together. The difficulties arising from this fact are aggravated by such conditions are as illustrated by the mixture of the Balanus and Macoma communities described on p. 289. These difficulties can be overcome only by the study of shores on which the communities are clearly differentiated and by the use of a transit to establish contours.

There have been a few important studies of communities on the shores of Australia and New Zealand (Hedley, '15; Oliver, '15, '23), but they differ materially from those of the northern hemisphere and comparisons are not easy. Considering the northern hemisphere where practicable, Appelöf ('12) and King and Russel ('09), Southern ('15) did not organize their observations on a community basis. Allee ('23) used the habitat in his studies at Woods Hole. In the area of his study the shore is low flat with scattered boulders affording a foothold for barnacles, etc. The difficulties are greater than in most localities, but doubtless the use of a transit to determine exact levels and studies elsewhere where the rock areas are of some size would help bring out the community relations more clearly. Beauchamp ('23) used the habitat as have many others. Colton ('16) recognized and differentiated communities on the coast of Maine. His littoral formation is not a formation but concerns the entire tidal region. "Formation" is entirely misused. Pearse ('13) refers merely to zones and considers the plants as a part of the habitat. The remaining work done on American waters including extensive work by the U. S. Bureau of Fisheries was not quantitative and was usually treated according to taxonomic groups, which resulted in a minimum of value from the standpoint of communities.

Investigators attempting to interpret the distribution of organisms are divisible into three classes: (1) Those who use the habitat; (2) those who stress large units and their subdivisions; (3) those who emphasize small units, frequently to the neglect of larger ones. The second group represent the view taken in the classification presented in this paper, which is similar to that of Petersen. There is a slight difference in the views of the large unit users however, some considering the biome or formation as the fun-

damental unit and others its first subdivision, the association (large unit sense). Both groups, however, recognize the same units.

The work of Petersen and his associates who recognized large units is noteworthy in three respects. First, Petersen did not start out to study communities but says they were forced upon him by his researches. Second, he and his associates used accurate quantitative methods throughout long periods. Third, their arrangement of communities is entirely parallel with those of the plant and animal ecologists, who use large terrestrial communities as fundamental units.

Petersen ('14) combined his smaller communities to form larger communities which are entirely comparable to the formation or biome (1915a Supplement to the 1914 annual report, with map). He drew a generalized map of the bottom communities of the North Atlantic based upon a study of the literature for the Atlantic in comparison with the work which he did himself. He combined several of the smaller communities which he had described to make the larger more generalized community. For example, Petersen combined (a) the *Brissopsis-Amphiura* communities (association), (b) *Echinocardium-Amphiura* community (association), (c) the *Haploops* community (faciation), and (d) the *Brissopsis-Ophioglypha* (association) to make the Brissopsis community (formation). The binding dominants are *Brissopsis lyrifera, Abra nitida, Axinus flexosus, Nucula tenuis, Ophioglypha albida, Leda pernula, Balanoglossus kuppferi, Leda minuta,* and *Pectinaria auricoma,* which are found in two or three or more of the four lesser communities (associations).

Petersen also recognized a major community (formation or biome) called the Venus community, covering much of the North Sea and bottom around the British Isles with an extension northward toward Iceland. Sparks ('29) examined the communities about Iceland and the Faroes and confirmed most of Petersen's anticipations. On about 50 km^2, Ford ('23) recognized the associations of the Venus community and found an additional community of different composition.

Davis ('23) finds the Venus community (biome) of Petersen covering the Dogger Bank in the North Sea. Still further paralleling of plant community phenomena on land is illustrated here. The Bank is characterized by "patches" in which the bivalve *Spisula subtruncata* is 10 to 20 times as abundant as any other species. It thus constitutes the chief dominant and presents a condition parallel to that found in the plant groupings called consociations.

The method of recognizing and designating communities is in strict accord with that of a large group of British and American plant ecologists. Clements' treatment ('20, p. 114) of the grassland, resulting from very similar

facts serves as an example. The writer shows Petersen's terminology in the foregoing statement with that used in this paper in parenthesis.

The work of two Swedish investigators, Gislen ('30) and Molander ('30), was done from the small unit viewpoint. The work of Gislen covers the epibioses of the Gullmar Fjord. These are the biotic communities on hard bottom. This paper includes an excellent and comprehensive summary of the history of the subject. Gislen presents some forty "associations" based on similarity of growth form. He follows the usual practice of algologists in calling every patch of different alga covering a square meter or less, a different *"association."* He refers frequently to sociological relations indicating that his viewpoint is primarily that of a plant sociologist.

A second Swedish investigator, Molander, has also investigated the Gullmar Fjord which Petersen studied and mapped in 1918. His viewpoint appears to be that of the small unit group. Possibly Molander's work was done in greater detail than that of Petersen. Petersen's map shows the following five communities: (1) Macoma; (2) Syndosmya (Abra); (3) Venus; (4) Echinocardium-filiformis; and (5) Brissopsis-chiajei.

On this area of 12 km^2 Molander recognizes nine associations, and including the faciations of these, a total of thirteen communities. He makes four or five communities out of the faciations of Petersen's ('18) Brissopsis-sarsii community (on clay bottom, depth 56-100 m). He further recognizes Petersen's Brissopsis-chiajei community and divides it into faciations; also Petersen's Echinocardium-filiformis community which he divides into three faciations. He also named an additional community which he designated in his introduction as quite distinct and different from others but which he says on page 33 is suggestive of Petersen's Echinocardium-Venus community.

Those animal ecologists who begin with the smallest units are usually students of the social insects or those who have studied the groupings of gregarious and other aggregating animals. A group of twenty-five Paramoecia is an aggregation, but has only a few social values of a herd of 10,000 or 1,000,000 bison, or a school of 100 sperm whales. Among students in this field, aggregation, association, society, colony, etc., are used quite often interchangeably, but usually in senses quite different from those indicated in this paper. Community, which is the accepted ecological term to apply to all of these, is rarely used.

The question of the use of the habitat or of communities, characterized by uniformly distributed species of size and importance in the description of the arrangement and distribution of organisms, is not being much debated at present. The use of the habitat is not supported by present investigation. It is, however, worthwhile to note Petersen's ('13) comments on this subject:

"At first it was thought possible to determine these zones by the depth alone or by a characterization of the vegetation and bottom conditions *(Pruvôt),* but though much has been gained along these lines we do not hereby come to the kernel of the matter, namely, the occurrence of the generally distributed animals, which alone can tell us where a certain animal community belongs, even though the depth and outer conditions may vary.

"Not even my own previous, laborious charting of all the different species in the Kattegat (Hauch) answered my purpose, partly because in this way I lost the general perspective and partly because dredges were used and all determinations of quantity had to be given up; but I had clearly realized the enormous difference between the various communities and have ever since sought for a method of characterizing the communities in a more synoptic manner that could be easily understood by others. I am now of opinion that I have found it (through the characteristic animals). . . ."

The findings of Huntsman ('18) concerned the distribution of animals, essentially tidal as a rule, near St. Andrews at the mouth of the Bay of Fundy. Balanus, Littorina and Mytilus are distributed over the center 5 m of the 8 m tidal range. The lower edge of their zone is overlapped for 1.0 m by Asterias, Strongylocentrotus and Buccinium. On the St. Lawrence side of the Cape Breton Island, Balanus, Mytilus and Littorina extend throughout most of the 1½ m tidal range and to a depth 18 or 36 m or more. Buccinium is restricted below 36 m and Asterias and Strongylocentrotus are few in number above this level.

Huntsman concludes that the peculiar conditions on the west shore of Cape Breton Island are due to the warm surface waters. He suggests that the barnacles and mussels do not go deeper near St. Andrews because of destruction by echinoderms and welks. The predator view as regards barnacle distribution is not supported by conditions about the San Juan Islands. *Balanus cariosus* and *B. glandula,* and *Mytilus edulis* do not extend below mean low tide. The place of the intertidal barnacles is taken by four or five other species. The same is true on the California coast. In the main body of the Strongylocentrotus-Argobuccinum community about the San Juan Islands starfishes are uncommon and could hardly affect the lower limit of Mytilus. Sea urchins are plentiful and are unlikely to distinguish species of Balanus (see pp. 281, 301, 308, and 309).

The question of controlling factor becomes of especial interest in this connection because of comparisons made possible by the studies of communities of the North Atlantic, Western Europe and Hudson Bay (by Shelford). Comparing all of these with Puget Sound one must conclude that the inferences which may be made at one place are likely to be contradicted at another. The truth is difficult to ascertain without the introduction of experimental methods along with the observations.

In this paper the writers have organized the discussion along lines which have stressed the principles governing the larger community units. They

have used important groups of species as indicators of conditions and of community limits. This is a distinct digression from the viewpoint from which most investigation in American waters has been conducted. The writers, however, believe that this is the most promising method of attacking the philosophic problems of nature as well as those of an economic bearing. The close parallel between the general phenomena brought out in the classical work of the Danish Biological Station and the work of plant ecologists is a further justification for the methods followed.

II. SUMMARY OF CONCLUSIONS

(1) Two subtidal communities of major rank (biome) occur in the area of study, one a large gasteropod-echinoderm community, the Strongylocentrotus-Argobuccinum biome (p. 280), associated with the more rapidly circulating waters, higher salinity, greater light penetration and less plankton, the other an annelid-bivalve community, Pandora-Yoldia biome (p. 265), in lower salinity, less circulation, slow fine silt deposition, and much bottom detritus. These general hydrographic conditions overshadow the type of bottom in determining the character of the community.

(2) The large bivalve-annelid community, Macoma-Paphia biome (p. 272), which is characterized by edible clams, is essentially subtidal though exposed at the lowest tides throughout its upper third. The success of the clams in its upper third and the height to which they occur is determined by the water holding capacity of the beach sands (also by inference from Danish communities, their size and abundance, by lack of destruction by fishes).

(3) The barnacle-mussel community, Balanus-Littorina biome (p. 289), which begins near mean low tide and reaches to a vertical meter or meter and a half above the upper limit of the Macoma-Paphia biome (mean high tide) is strictly tidal. Its presence is governed almost as much by water movement as by substratum as mussels may form a bed in still water on the upper portions of a sand beach and constitute a substratum for the attachment of barnacles. They thus build up the entire community. This leads to a mixing and competition between the Balanus-Littorina and Macoma-Paphia biomes (p. 289).

(4) The pelagic community (including both plankton and nekton) has an important effect on the subtidal communities chiefly in influencing the penetration of light and the amount of detritus supplied to the bottom (pp. 259, 265, 266).

(5) The evidence gathered from all sources indicates that the general hydrographic conditions (submarine climate) are more important than kind of bottom materials in determining the character of benthic communities (p. 290, see also p. 345).

(6) The arrangement of species on the bottom especially in the Balanus-

Littorina biome is controlled by seeding and survival in relation to combinations of tide, temperature and sunshine. The exact arrangement has significance only when taken together with the series of events producing it. It is quite inexplicable and without significance when approached without details as to preceding events. The observations of Rice demonstrated this for tidal barnacles (p. 293). Variations in the relative position of maximum abundance for the various clams on different beaches and in different years suggest the same relation for them. The same principle probably holds good for the strictly subtidal communities (see 7 below).

(7) The quantity per unit area of any or nearly all the species in the communities studied may fluctuate from season to season, from year to year, or over longer periods. Argobuccinum was very abundant in 1922 when the original work on the Strongylocentrotus-Argobuccinum biome was done. By 1926 it was almost absent but gradually increased to 1930 when observation ceased. In the Pandora-Yoldia biome there was a decline in numbers of Pandora, Yoldia, and Marcia and an increase of Scalibregma (p. 271). The behavior of several other species is similar.

(8) Succession or development of communities has been but little studied. The period of development of Balanus-Littorina communities is evidently not longer than the few months suggested by Pierron and Huang. (Rice found, p. 295, that barnacles do not set well on stones that have not been in sea water.) Development of the Macoma-Paphia biome is evidently rapid on sand beaches (p. 278). Succession is evidently slowest where suitable soils or other substrata must be built up with the aid of organisms, *e.g.*, in the Strongylocentrotus-Argobuccinum biome where a bottom of shells must be built on mud or sand bottom (p. 288) and the Pandora-Yoldia biome, a bottom of mud with much detritus is necessary. All the communities studied are characterized by short life histories and rapid replacement; hence, also rapid development and quick response of community composition to minor changes in external conditions. Most of the communities studied are essentially climax.

(9) The study of East Sound, which is evidently being slowly filled chiefly with organic detritus, shows the large effect of hydrographic conditions in the production of much plankton, etc., and the accumulated reaction of organisms on the habitat with resulting changes in community composition. It is evident that the suggested closing of a passage shutting tidal circulation out of the sound could change hydrographic conditions so as to produce all the noteworthy differences between the communities in the upper end of the sound and the Strongylocentrotus-Argobuccinum biome north of Orcas Island (pp. 312 and 318).

(10) The writers are convinced that organisms, or more especially community groupings of organisms, are the best indicators of hydrographic con-

ditions (submarine climate and weather) and that the success or failure, presence or absence, scarcity or abundance of these living things is correlated with determinable physical and chemical conditions. To yield the best results, the study of conditions and of communities must go hand in hand, but also the nature of the study of conditions must constantly be moulded by a study of the correlation of the responses of organisms with the knowledge of conditions already gained. In other words, biological oceanographic research should not be planned and executed as a technological or engineering project. Beyond a certain point and also probably even at the beginning so-called physical oceanography must take account of the responses of organisms and use them as guides in elaboration of the program. When their responses are understood organisms may be used to extend the generalization of a purely physical survey. The bottom communities are fully as important in this respect as pelagic ones. We are convinced that certain combinations of intertidal species may be used to indicate average salinity of the surface waters (Fig. 1 and p. 290).

(11) The necessary background for pursuing ecological work in the sea cannot be acquired in laboratories or in specialized courses dealing with particular groups of marine organisms. If oceanography is to progress, men will have to be trained through a broad general contact with the physical and chemical conditions and the occurrence and responses of organisms. Instruction of this type is rarely available.

(12) The geographical extent of the major communities is relatively unknown except for the Balanus-Littorina biome.

A. *Balanus-Littorina Biome*

General circumpolar occurrence of Mytilis edulis as an important dominant in parts of the North Pacific and entire Atlantic, and the similarity of dominant life forms, general equivalence of species in both the North Atlantic and North Pacific leads to the conclusion that communities of the Balanus-Littorina biome type cover much of the suitable shores of the northern hemisphere. They are divided into several associations, each with several faciations. The southern hemisphere apparently has different communities.

B. *The Macoma-Paphia biome* (p. 277) is evidently not found in the Atlantic. According to Newcombe ('35) Mya and Nereis are the dominants in the Bay of Fundy and Venus is important farther south. *Mya arenaria* was introduced into the Pacific and while *Macoma balthica,* an important species in Europe, occurs in the area it is of secondary importance. Communities of the general type of the Macoma-Paphia biome occur over the northern hemisphere at least.

C. *The Strongylocentrotus-Argobuccinum biome* (p. 287) is evidently

a North Pacific community. Echinoderm-large gasteropod communities occur, however, in the Atlantic. The communities of Vineyard Sound apparently approach this type.

D. *The Pandora-Yoldia biome* (p. 269) is also evidently limited to the North Pacific. The Abra (Syndosmya) community near Denmark is of this type and it is also probable that one occurs in Buzzards Bay (Mass.).

(13) The tension line between the terrestrial and marine communities is usually associated with the Macoma-Paphia biome. Successions to land occur in nearly-cut-off pools. There are probably several routes to land communities but the invasion of Salicornia on high spots leading to hummocks of Salicornia followed by sedges and grasses is common (pp. 319, 324).

(14) The physiological characters of the animals of the various communities differ strikingly in accord with (a) the general conditions of community habitat and (b) the habits as regards the level occupied by the species (pp. 264, 271, 279, and 289). (See also Shelford, '16.)

(15) Studies of the resistance of animals of different ages (Andrews, '25) and the researches of Rice (p. 295) indicate that life history studies should be carried on under controlled conditions. They should be accompanied by experimental investigation of the sensitivities of the different stages. Field researches which correlate the ever changing physical, chemical and biological conditions of the habitat with the status of species of importance in the communities in question must form the guide for experimental work both out of doors and in the laboratory, *i.e.*, the responses of organisms and not imitation of physical and chemical methods or the easy operation of commercial devices should dictate the experimental conditions imposed.

PART II

A STUDY OF THE ANIMAL COMMUNITIES OF A RESTRICTED AREA OF SOFT BOTTOM IN THE SAN JUAN CHANNEL[1]

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I. INTRODUCTION

The bottom communities of the San Juan channel and adjacent areas have been reported upon by Shelford and Towler ('25), and also by Perry ('16) and Essex and Steggerda ('25), who restricted their attention to hard bottom communities. Shelford (p. 258) surveyed the biomes about the San Juan Islands and reported a new major community on mud bottoms near Olga and the mainland.

In 1926 the writers made a detailed study of the animal population of a restricted area, see station 51, Fig. 1, p. 254, which lies within the hard bottom region previously surveyed by Shelford and Towler ('25). The purpose was (1) to throw light on the distinctness of two major communities, the Strongylocentrotus-Argobuccinum and the Pandora-Yoldia communities, (2) to determine the relative importance of the character of the bottom as compared with the physical and chemical qualities of the water above it, (3) to ascertain the community composition in and on mud bottom, as compared with that associated with the rocks in the adjacent areas, and (4) to establish the lower limits of the clam beach community (Macoma-Paphia biome) which Peterson ('18) has said would reach 30 meters if it were not for competition.

The area studied was 195 meters wide and 377 meters long. It extended from the shore of Brown Island toward the present station site, terminating in mid-channel (Fig. 11). The southeast and south corners were identified by means of points on the shore, while buoys were anchored to mark the north and northwest corners.

The contour of the bottom was determined by soundings and readings from a meter wheel which operated in connection with the bottom sampler cable. A contour map was prepared from the assembled data (Fig. 12).

The nature of the bottom of the area of study was determined from materials brought to the surface by the bottom sampler and dredge. The quality of the bottom and the distribution of most of the plant life is indicated in Fig. 13. It was composed primarily of mud and fine sand with a few shells

[1] Contribution from the Lawrence, Kansas, Junior High School, the Science Department, Edinburg College, Edinburg, Texas, the University of Illinois, and the Puget Sound Biological Station.

and pebbles included locally. Occasionally small boulders were found, especially in the areas containing kelp (Fig. 13). The bottom of the north corner was composed of black mud and molluscan shells.

A few outcroppings of rock were encountered in the 12 to 16 meter levels. The collections from the rocks did not include the important species from

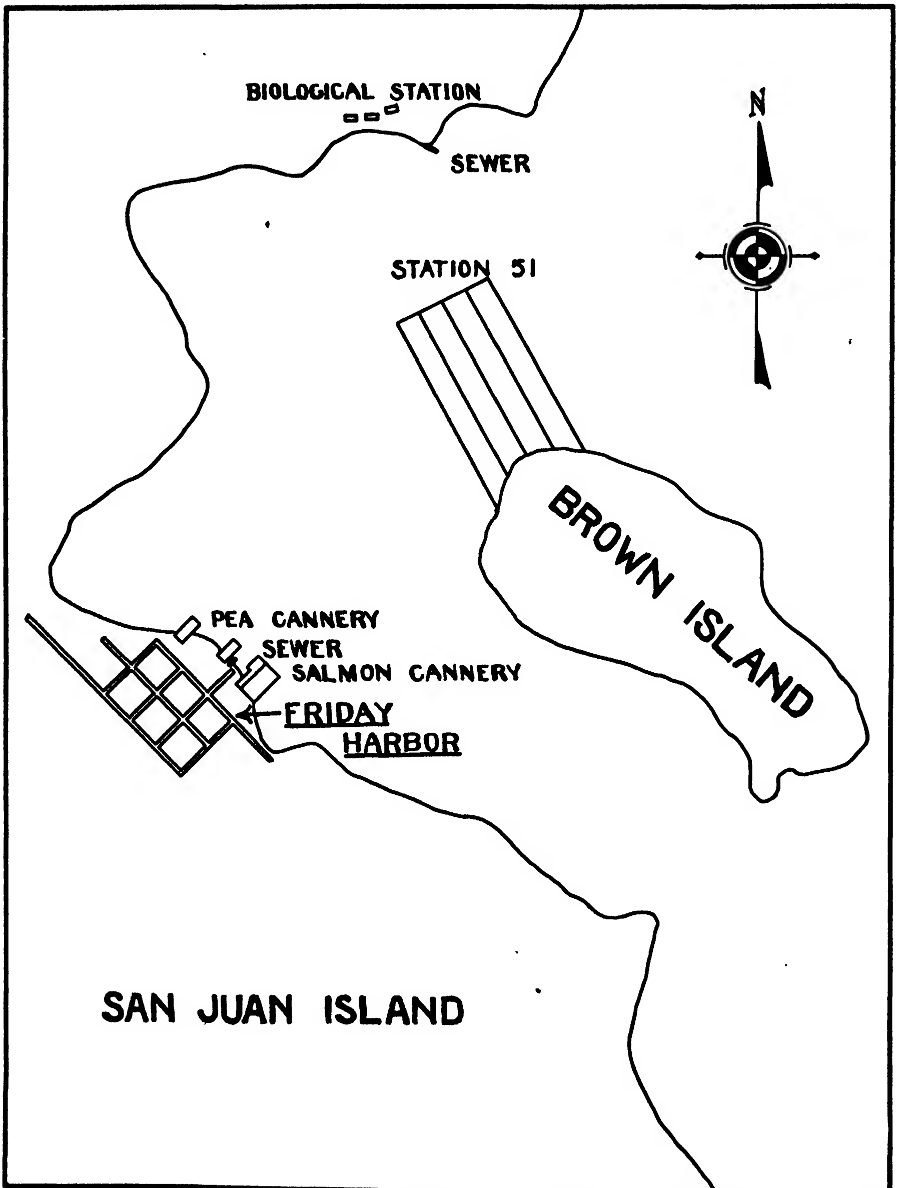

FIG. 11. Showing the location of station 51 in relation to Brown and San Juan Islands.

which conclusions are drawn, except for two or three individuals. The remainder of the rock collections were of no particular ecological significance due to their infrequent occurrence.

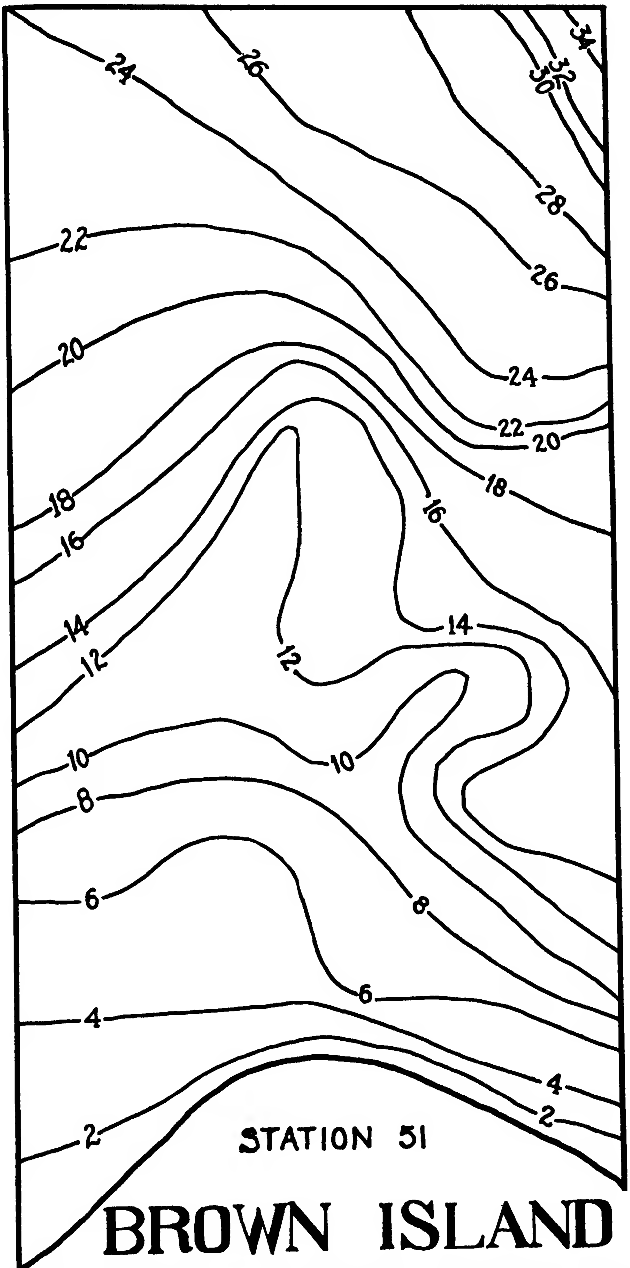

FIG. 12. Showing the bottom contour of the area. Lines indicate depths in meters, measured from mean low tide.

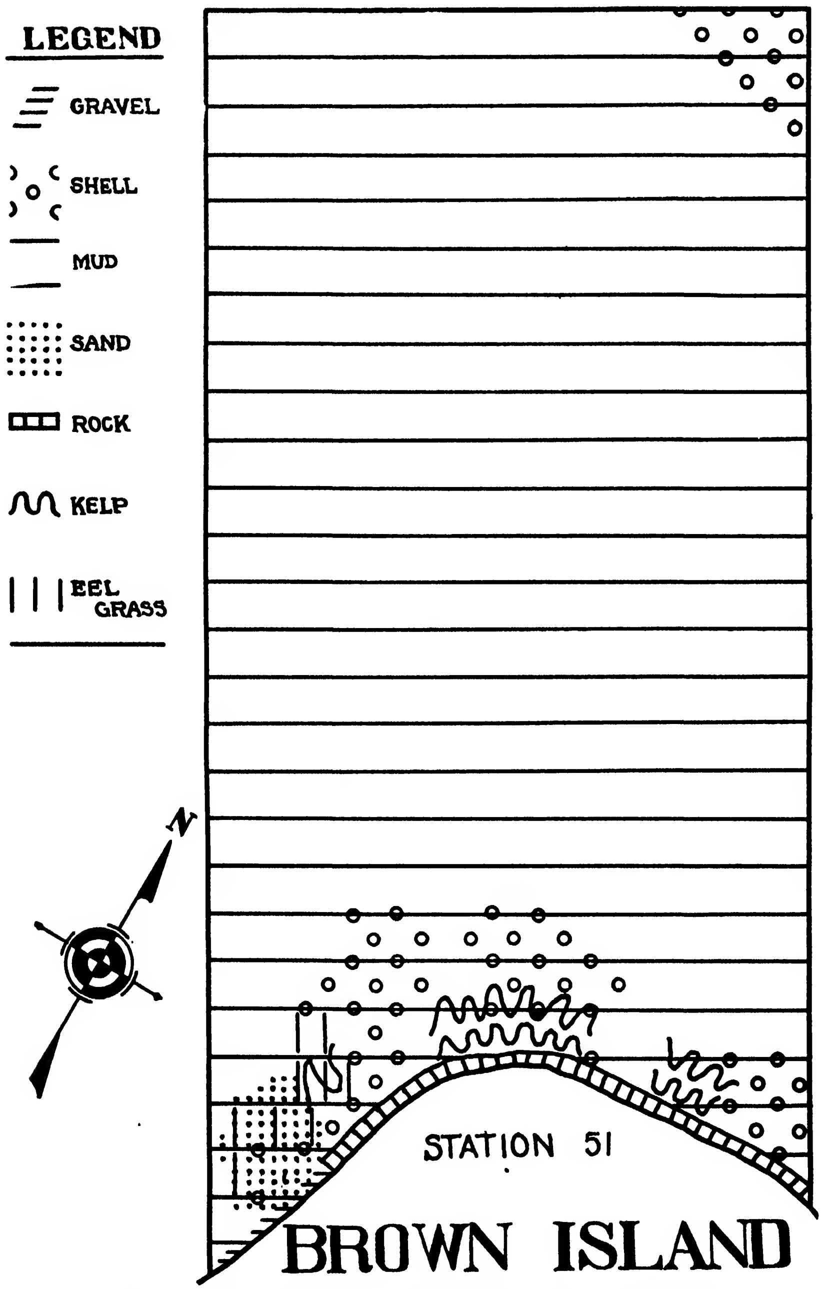

FIG. 13. Indicating the composition of the bottom and the distribution of kelp and eel grass within the area studied.

A considerable amount of Nereocystis (kelp) was found at two to six meter depths, especially off the rockier portions of the shore. Detached fronds or whole plants of other species of algae were encountered below a depth of twelve meters. Zostera (eel-grass) was abundant in a restricted area in the south corner.

The shoreline was rocky, especially in the 1 to 1.5 m between the upper limit of clams and high tide. This belt was partially covered with barnacles and harbored many motile tidal species. No account was taken of this belt.

(1) Methods of collecting and determining number of specimens.

A measured total of one square meter of sea bottom was brought to the boat's deck at each of fifteen substations (I-XV, Fig. 14) by means of a Petersen bottom sampler of 0.1 m^2 capacity. The organisms were washed free of mud and detritus in 2 mm mesh sieves.

Kelp holdfasts totaling 1.5 square meters were dislodged from the bottom by pulling on the plants from the stern of a rowboat. The surface area of stones, etc., brought up in this manner was measured with a ruler.

A naturalists' dredge and a trawl were towed over various parts of the area (a-p, and 1-3, Fig. 14). The dimensions of the dredge frame were 1.15 meters by 0.55 meters. Those of the trawl were 1.9 meters by 0.5 meters. Both nets were of one inch mesh. The distance over which these instruments were towed was estimated by noting positions of the boat in relation to various points on the shore.

TABLE 16. Showing efficiency of dredge and trawl at various stations.

Dredge		*Trawl*	
Haul	Per Cent Efficiency	Haul	Per Cent Efficiency
a.	4.57	1.	41.35
e.	0.29	2.	1.53
g.	0.63	3.	0.52
j.	4.56		
k.	0.53		
l.	1.30		
n.	8.47		
p.	0.89		

Average efficiency, 2.65 per cent.

The efficiency of the dredge and trawl was estimated at various stations by comparing their catches of non-motile or slow-moving species qualitatively and quantitatively with those of the bottom sampler for the same area and averaging all values thus derived for these species. The sampler was assumed to be 100 per cent efficient (Kirsop, '22, has estimated it to be 95 per cent efficient on mud bottom). An average efficiency of the dredge or trawl for the entire plot could have been estimated by assembling all efficiency data according to species and without reference to stations. The value for average trawl efficiency used in this study was derived by averaging all calculated station values. It is 2.65 per cent. This estimate was used in computing the number

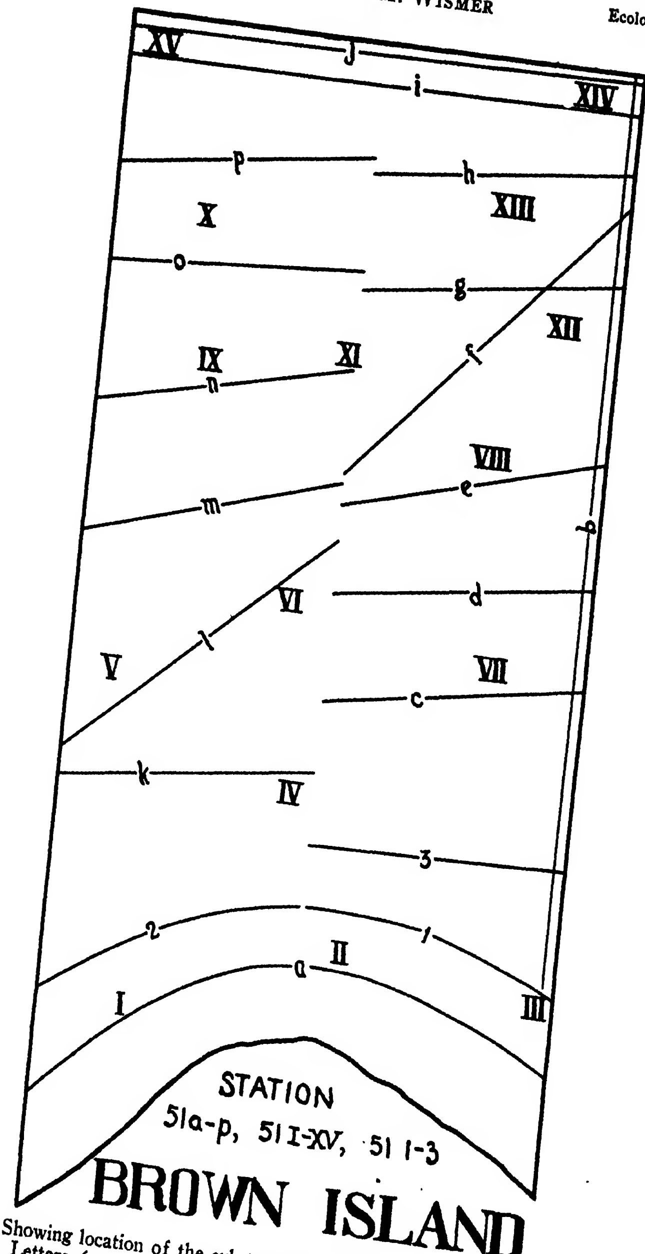

FIG. 14. Showing location of the substations of station 51 for the use of the various instruments. Letters (a-p inc.) refer to dredge hauls; Roman numerals (I-XV) refer to bottom sampler stations; Arabic numerals (1-3) indicate hauls made with a rock trawl.

of animals at stations where a very small number of non-motile forms were collected by the apparatus.

The high efficiency of the trawl at station 1 as compared with that at stations 2 and 3 is referable to differences in the amount of vegetation encountered. Many animals living at the depth represented by station 1 are found in and on vegetation and they readily fall into the collecting device. In comparing stations 2 and 3 it must be remembered that as depth of the water increases the pull of the cable becomes increasingly effective in causing the instrument to skip over specimens.

The efficiency of the dredge at various stations is seen to vary within a wide range (Table 16). This is referable to (1) differences in relative length of cable let out while the instrument was in tow, (2) differences in the slant of the sea bottom in relation to the direction of pull of the cable; a dredge will usually collect more effectively if it is pulled up a slope than if it is pulled down one, and (3) the amount of vegetation encountered. Thus at substations *i* and *n*, where vegetation was denser than at all other relatively deep water points, the values for efficiency were higher than at any other outshore stations at which an estimate was made. Despite the presence of vegetation at lower levels, especially at the above stations, there is evidence to support belief that efficiency decreases slightly with depth, as may be seen in Fig. 15.

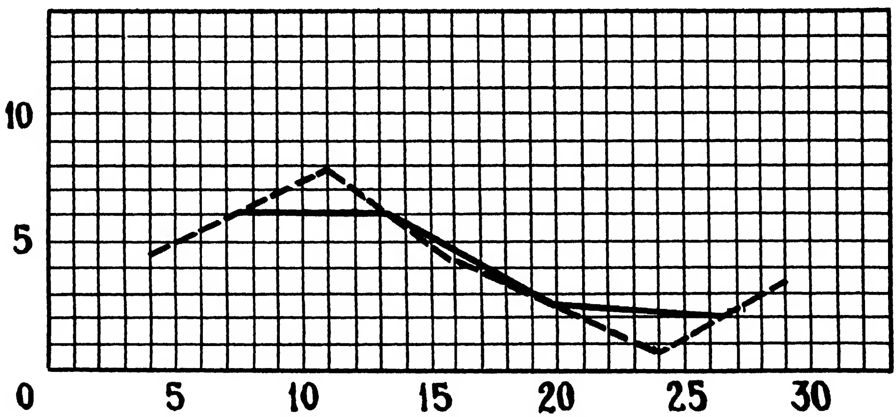

FIG. 15. Showing efficiency of the dredge plotted against depth. The broken lines connect points representing averages for depth of 4, 11, 24, and 29 m. The unbroken lines connect the mid-points in the broken lines and suggest a lowering of efficiency with increasing depth.

II. QUALITATIVE AND QUANTITATIVE DATA

All specimens collected in the area and the abundance of each at various levels are indicated in Tables 17, 18, and 19 below. Unfortunately the worms were lost before identification was complete. The available data pertaining to them is presented merely for its quantitative value.

Fishes move rapidly as compared with most other animals and readily escape from collecting devices. Furthermore, differences in habits and reactions of various species tend to make any collection equipment selective. The area covered by the dredge and trawl hauls ranged from 180 to 230 m^2. The average was about 200 m^2. The number of fishes of each species taken in each haul was reduced to a number that might have been caught in a 200 m^2 haul if the apparatus had taken fishes at the same rate. This made only a small change in most of the figures. To avoid the resulting fractions they

TABLE 17. Showing dominants and slow-moving influents of the area of study (Station 51) together with taxonomically related forms.

The figures indicate the estimated numbers of individuals per $10m^2$. ‡ marked items are estimates from dredge and trawl hauls. Column 1 represents a depth range of 2-6 m and includes dredge haul *a*, trawl haul 2 and bottom sample substation 1 (Fig. 14). Column 2 covers a depth range of 8-12 m. Data included are from trawl haul 1, dredge haul *l* and bottom sampler substations 3, 4, 5, and 6. Column 3 covers bottom sampler substation 7 and dredge hauls *c, d, e,* and *n*. The depth range is 11-20 m. Column 4 represents dredge hauls *o* and *p* and bottom sampler substations 8 and 9. The depth range is 21-26 m. Column 5 includes bottom sampler substations 12 and 13 and dredge hauls *g* and *h*. The depth range is 21-33 m. Column 6 represents all depths greater than 24 m. Bottom sampler substations 14 and 15 and dredge hauls *i* and *j* are included. Species considered dominants and slow moving influents are indicated by †.

Species	Column					
	1	2	3	4	5	6
STARFISHES						
†*Orthasterias columbiana* Ver.	....	....	....	....	6	1
Ophiopholis aculeata (Linn.) Gray (brittle star)	....	....	....	....	....	12
Evasterias acanthostoma Ver.	....	....	....	....	....	11
Luidia foliolata Grube (fragile star)	....	....	....	....	....	1
SEA CUCUMBERS						
Cucumaria sp. (white cucumber)	20	90	2	....	....	....
†*Stichopus californicus* Ed. (large red cucumber)	....	....	....	....	6	28
SEA URCHINS						
†*Strongylocentrotus drobachiensis* Müller (green urchin)	100	22	36	52	26	22
†*Strongylocentrotus franciscanus* A. Ag. (red urchin)	....	....	....	4	12	4
MUSSELS, CLAMS, PECTONS, ROCK OYSTERS						
Macoma sp.	12	....	....	....	....	....
Cardium corbis Martyn (cockle)	18	50	10	....	....	....
Modiolus modiolus Linn.		20	....	....	10	10
Paphia staminea Conrad	8	40	....	30	....	....
Cardium californiense Desh.	2	80	38	10	30	30
Marcia subdiaphana Carpenter (thin shelled clam)	9	40	....	80	10	66
Venericardia ventricosa Gould	30	1‡	....	....	20	130
Nucula castrensis Hinds, (camp nutshell)	2	....	....	....	....	450
Macoma nasuta Conrad, (bent nose clam)	10	80	....	....	40	....
Macoma secta Conrad	....	13‡	....	....	....	....
Macoma yoldiformis Carp.	....	20	....	....	....	....
Yoldia scissurata Dall	....	168‡	20	110	10	960
Yoldia ensifera Dall	....	44‡	30	10	....	83
Solen sicarius Gould	....	10	....	10	10	30
Pandora filosa Carp. (asymmetrical bivalve)	....	20	....	....	....	30
Phacoides tenuisculptus Carp.	....	....	....	100	....	....
Yoldia myalis Couth.	....	....	....	....	....	60
†*Pecten hindsii* Carp. (scallop)	2‡	7‡	....	21‡	....	22‡
†*Pecten hericius* Gould (scallop)	....	4‡	62‡	59‡	28‡	60
Pododesmus macroschisma Desh.	20	13	....	10	10	20

TABLE 17 (Continued)

Species	Column 1	2	3	4	5	6
BARNACLES						
†*Balanus pugetensis* Pil.	360	88‡	....	....	....	22‡
Balanus sp.	....	11‡	....	....	....	....
†*Balanus nubilis* Dar.	....	4‡	....	....	....	20‡
†*Balanus rostratus* Hoek	....	....	....	248‡	10	....
TUNICATES						
Pyura haustor (Stim.)	2‡	10	....	....	....	....
Styela gibbsii (Stim.)	2‡	....	....	....	10	2‡
Boltenia villosa (Stim.)	....	....	....	38‡	6‡	1‡
Corella willmeriana Herd.	....	....	....	11‡	....	6‡
SNAILS, LIMPETS, CHITONS, NUDIBRANCHS, SLIPPER SHELLS						
Nitidella gouldii Carp.	....	30	....	40	....	30
Margarites lirulatus Carp.	360	80	....	20	....	....
Chrysodomus tabulatus Baird	94‡	80	....	23‡	....	22‡
Lacuna divaricata Fab.	440	147	....	....	....	100
Margarites pupillus Gould	1460	122	....	22‡	....	10
Polinices pallida Brod & Sow.	4‡	570	....	34‡	60	30
†*Trichotropis cancellata* Hind.	....	130	....	....	....	....
Calliostoma variegatum Carp.	....	30	....	12‡	30	....
Calliostoma annulatum Martyn	....	....	....	3	....	....
Searlesia dira Reeve	4	17	....	....	63	4
Acmaea mitra Esch.	12	39	....	....	....	....
Acmaea asmi Mid.	....	21	....	....	....	....
Mopalia ciliata Sow.	2	....	....	....	....	....
Lepidochitona lineata Wood., (painted chiton)	5	24	....	....	....	....
Melibe leonina Gould	3	....	....	....	....	....
†*Calyptraea fastigiata* Gould, (Chinese hat)	24	30	17	30	76	160
†*Crepidula nivea* C. B. Adams	2	61	8	....	10	22
WORMS						
Nemerteans	40	20	....	....	....	....
Sternaspis fossor Stimp.	....	90	....	....	....	30
Nereidae, Nephthydidae, etc.	48	1120	130	300	100	138
Other Errantia	14	70	....	10	10	....
Sedentaria	16	360	60	270	30	23
Turbellaria	....	10	10	70	....	....
TOTAL (worms only)	118	1670	200	650	140	191

were multiplied by 10 and hence represent the fishes that might have been taken on 2000 m^2 under similar conditions if caught at the same rate.

III. MAJOR COMMUNITIES

(1) MACOMA-PAPHIA BIOME

The following dominants and influents which are known to characterize the Macoma-Paphia biome (clam beach community) at or near the low tide line were found:

Macoma nasuta Conrad, bent-nosed clam.

Macoma secta Conrad, clam.

TABLE 18. Invertebrate influents found in the area—Station 51.
For interpretation of column headings see Table 17.

Species	Column 1	2	3	4	5	6
SHRIMPS						
Pandalus danae Stim.	1‡	147‡	1049‡	67‡	129‡	67
Spirontocaris prionota (Stim.)	.....	4‡	10	.....	.....	6
Pandalus stenolepis Rath.	.....	238‡	359‡	188‡	1248‡	55‡
Crago alaskensis (Lock.)	.....	242‡	414‡	315‡	621‡	65‡
Paracrangon echinata Dana	.....	2‡	68‡	36‡	229‡	150‡
Spirontocaris groenlandica (Fab.)	.....	2‡	34‡	63‡	2	105‡
Spirontocaris tridens Rath.	.....	7‡	32‡	2‡	9‡	14‡
Spirontocaris suckleyi (Stim.)	.....	14‡	132‡	521‡	.....	.....
Spirontocaris kincaidi Rath.	.....	.....	362‡	33‡	.....	.....
Pandalus sp.	.....	.....	4‡	.....	75‡	2‡
Pandalus hypsinotus Brandt	.....	.....	452‡	332‡	9‡	102‡
Crago munita (Dana)	.....	.....	.....	.....	12‡	7‡
CRABS						
Pagurus granosimanus (Stim.) hermit crab	20	.....	.....	.....	.....	.....
Telmessus cheiragonus (Til.), Rath., hermit crab	100	.....	.....	.....	.....	.....
Pagurus beringanus (Bened.), hermit crab	20	3‡	.....	.....	.....	.....
Cancer productus Rand, edible crab	100	100	.....	.....	.....	.....
Oregonia gracilis Dana, decorator crab	21‡	67‡	20	.....	42‡	.....
Pagurus tenuimanus (Dana)	2‡	4‡	.....	.....	8‡	11‡
Pagurus alaskensis Bened., hermit crab	10	2‡	.....	10	18‡	14‡
†*Cancer oregonensis* (Dana) Rath., hairy cancer crab	1‡	53‡	40‡	102‡	7‡	15‡
Pugettia gracilis Dana, graceful crab	20	14‡	5‡	15‡	7‡	44‡
Epialtus productus Rand., kelp crab	100	66‡	5‡	.....	2‡	14‡
Pagurus hirsutiusculus (Dana), hermit crab	110	5‡	10	.....	.....	6‡
†*Hyas lyratus* Dana	.....	69‡	212‡	10	20	57
Paguristes turgidus (Stimp.), hermit crab	.....	8‡	6‡	.....	.....	2‡
Pagurus dalli (Bened.), hermit crab	.....	121‡	15‡	.....	.....	.....
Pagurus splendescens Owen, hermit crab	.....	.....	8‡	.....	1‡	2‡
Pagurus kennerlyi (Stimp.), hermit crab	.....	.....	.....	143‡	.....	2‡
Pagurus ochotensis Brandt, hermit crab	.....	.....	.....	.....	.....	2‡
AMPHIPODS AND ISOPODS						
Caprella sp.	240	.....	.....	.....	.....	.....
Idotea resecata Stim.	154‡	.....	.....	.....	.....	.....
Idotea wosnesenskii Brandt	38‡	.....	.....	.....	.....	.....

‡Values calculated from catches of dredge or trawl.

Macoma sp., clam.
Cardium corbis Martyn, cockle.
Paphia staminea Conrad, little neck clam.
Pagurus granosimanus (Stim.), hermit crab.
Pagurus beringanus (Bened.), hermit crab.
Telmessus cheiragonus (Til.), hermit crab.
Cancer productus Rand., cancer crab.

The distribution and abundance of species characteristic of this community emphasizes the fact that it is essentially *sub-tidal* although it survives in the soil water of exposed beaches up to a meter or more above mean low tide. Its lower level is shown by our data to lie at a depth of approximately ten

TABLE 19. Showing vertebrate influents found in the region.

Values indicate estimates per 2000 m² based on dredge and trawl catches. Column 1 represents depths of 2-6 m; column 2, depths of 8-12 m; column 3, depths of 11-20 m; column 4, depths of 21-26 m; column 5, depths of 21-33 m; column 6, depths of 24-34 m.

Species	Column					
	1	2	3	4	5	6
INFLUENT FISHES						
Rhinogobiops nicholsii (Bean), small fish	....	17	....	....	....	....
Hippoglossoides elassodon J. &. G., flounder	....	8	....	....	....	....
Lyconectes aleutensis Gilbert, red devil	....	8	....	....	....	....
Pholis ornatus (Girard), chameleon blenny	....	8	....	....	....	....
**Rhamphocottus richardsoni*, Günther, grunt fish	....	8	....	....	....	....
Pleuronichthys coenosus Gir., flounder	....	8	18	....	....	....
Hemilepidotus hemilepidotus (Til.), red sculpin	....	....	18	....	....	....
**Myoxocephalus polyacanthocephalus* (Pal.), great sculpin	....	....	18	....	....	....
Eumicrotremus orbis (Gunther), warty lump sucker	....	....	18	....	....	8
**Icelinus borealis* Gil., northern sculpin	....	....	18	....	....	26
Chitonotus pugetensis (Steindachner), rough backed sculpin	....	....	35	17	....	7
Lepidopsetta bilineata (Ayres), rock flounder	....	....	89	53	26	8
Nautichthys oculofasciatus (Gir.), sailor fish	....	....	....	18	....	....
Hypsagonus quadricornis (Cuv. & Val.), sea poacher	....	....	....	2	....	....
Dasycottus setiger Bean, woolly sculpin	....	....	....	8	....	....
Blepsias cirrhosus (Pallas), silver spot sculpin	....	....	....	8	....	26
Odontopyxis trispinosus Lock., pitted sea poacher	....	....	....	18	....	35
Careliparis dennyi (Jor. and Starks), sea snail	....	....	....	....	8	....
Xeneretmus triacanthus (Gil.), sea poacher	....	....	....	....	....	35

*Forms considered influents by Shelford (see p. 282.)

meters below mean low tide. Maximum abundance of animals is sub-tidal. The ecotone between the Macoma-Paphia and the Strongylocentrotus-Argobuccinum biomes covers depth ranges from approximately three to ten meters, measured from mean low tide.

(2) STRONGYLOCENTROTUS-ARGOBUCCINUM BIOME

The Strongylocentrotus-Argobuccinum biome (a community of large echinoderms and mollusks) presented a modified composition or faciation within the area studied. All dominants and slow-moving influents listed by Shelford, p. 281, as usually present throughout this biome were encountered with exception of the following:

Argobuccinum oregonensis Red., snail.
Calliostoma costatum Martyn, snail.
Psolus chitonoides Clark, sessile cucumber.
Amphissa columbiana Dall., snail.
Cucumaria miniata Brandt, sea cucumber.

In this particular year Argobuccinum was at a low point in its abundance but it is common on such bottoms in years of abundance. From the usual distribution of Calliostoma and Amphissa there appears to be no reason for absence except a scarcity which caused them to escape collection. Psolus and *C. miniata*, however, are associated with rocks which are wanting in the area.

a. Cardium-Solen faciation of the Strongylocentrotus-Pugettia association (characterized by *S. franciscanus* and *P. gracilis*)

The place of the four Strongylocentrotus-Argobuccinum dominants noted above was taken by such forms as *Cardium californiense* Carp., *Yoldia scissurata* Dall, *Solen sicarius* Gould and *Venericardia ventricosa* Gould. Cardium is most uniformly distributed and is easily recognized. It is nearly always found on muddy bottom within the biome. Solen is less abundant, but is a characteristic form in the area. Hence, these species are given recognition in the naming of the faciation.

b. Algal faciations

Both types of algae which were used by Shelford, Part 1, p. ???, to designate faciations occur in the area, but their distribution was such that differentiation between the animal populations associated with them was impossible. Brown and red algae found in or near mid-channel were:

Brown Algae	*Red Algae*
Laminaria sp.	Callophyllis sp.
Alaria sp.	Nitophyllum sp.
Agarum sp.	Gracilaria sp.
Cymatheria sp.	
Desmerestia sp.	
Monostroma sp.	

(3) PANDORA-YOLDIA BIOME (ABSENT)

Although representatives of the Pandora-Yoldia biome might have been expected on a mud bottom such as was dealt with in this study, the four dominants and slow-moving influents (Shelford, see p. 283) listed below were not encountered:

Scalibregma inflatum Rathke.
Yoldia limatula Say.
Pycnopodia helianthoides (Br.).
Cucumaria populifera (Stimp.).

Three of the remaining four were far less numerous than Shelford or Weese (cf. Table 13, p. 316) found them at corresponding depths during the same year, as shown in Table 20 below.

TABLE 20. Showing abundance of certain Pandora-Yoldia dominants within the area as compared with their abundance within the biome in 1926.

Species	Number per 10 m² on plot here studied	Number per 10 m² from Shelford's data for corresponding depths see Table 1, 271 also p. 269
Marcia subiaphana Carp.	9–80	16
Yoldia ensifera Dall	10–93	541 {Y. ensifera and Y. limatula
Sternaspis fossor Stim	30–90	200
Pandora filosa Carp	20–30	350

Marcia subdiaphana Carp. is the only one of these species with a wide distribution over the area. None of the species which Shelford (see p. 265) considers characteristic of the Pandora-Yoldia biome were collected. This community is not regarded as present in the area of study.

IV. CONCLUSIONS

1. The Strongylocentrotus-Argobuccinum biome, large echinoderm-mollusk community, covers muddy bottoms within its climatic area. Certain species are missing, however, and forms which are characteristic of such areas within the biome take their places.

2. Only a few species characteristic of the Pandora-Yoldia biome, small bivalve worm community, occur in isolated mud bottom regions within the climatic area of the Strongylocentrotus-Argobuccinum biome. They are found in reduced numbers there as compared with the biome in which they are dominants.

3. The lower limit of the Macoma-Paphia biome, clam beach community, is established at a depth of approximately ten meters.

4. The ecotone or transition which involves the Strongylocentrotus-Argobuccinum and Macoma-Paphia biomes covers a depth range of 3 to 10 m, measured from mean low tide.

5. In general terms the study when compared with the work of Shelford, Part I, p. 290, shows that the circulation and general condition of the water, together with correlated factors such as amount of plankton, amount of detritus, decomposition products, and oxygen, control the communities present on bottoms classified as mud to a greater extent than the observable character of the mud itself. The organisms constituting the prevalents or most abundant constituents of the community are better indicators of conditions than physical instruments. The use of instruments and measurements should not be neglected, however.

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SOME PRINCIPLES OF COMPETITION AS ILLUSTRATED BY SUDAN GRASS, *HOLCUS SORGHUM SUDANENSIS* (PIPER) HITCH.

By

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SOME PRINCIPLES OF COMPETITION AS ILLUSTRATED BY SUDAN GRASS, *HOLCUS SORGHUM SUDANENSIS* (PIPER) HITCH.*

INTRODUCTION

No student of field ecology can doubt the fundamental importance of competition either in the development of natural vegetation or in the production of cultivated crops. There is great need, however, of replacing qualitative knowledge of competition by experimental, quantitative data. This is especially true in studies of crop plants where, with few exceptions, only the final results of competition, as expressed by yields, have been determined. Sudan grass was suggested as an excellent plant to use in studying the principles of plant competition. It grows so rapidly that it uses large amounts of water and nutrients and the shade cast is such that competition for light soon becomes an important factor.

The history of the competition concept has been given by Clements, Weaver, and Hanson (1929) in their monograph on competition. This includes a statement of the earliest views; modern experimental studies, including materials furnished by investigators on plant succession; and a special statement of plant competition in forest and cultivated fields. They point out that competition in field and garden differs in two important respects from that in natural communities. It is, in the absence of weeds, between the individuals of one species or variety, and the habitat is controlled in as large a degree as possible in favor of the crop. These writers, by their work in field and garden, have also contributed in a large measure to the knowledge of competition of crop plants begun by Montgomery (1910, 1912), extended by Kiesselbach and coworkers (1918, 1923, 1928, 1933), and furthered by numerous other investigators. Because of their historical analysis, a further summary of the literature at this time is unnecessary.

As understood by the writer, competition is purely a physical process. It is essentially a decrease in the amount of water, nutrients or light available for each individual, and therefore increases with the density of the plant population. With few exceptions, an actual struggle between two plants never occurs.

The writer is under deep obligation to Dr. J. E. Weaver for outlining the problem and for efficient direction throughout the entire course of the work.

Selection of Plots

An area of moderately low, level land, on the flood plain of Salt Creek, and two miles north of the Capitol Building in Lincoln, Nebraska, was

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selected for these studies. The field, which had been farmed for only a few years, was originally a part of the Belmont prairie. It was selected because both soil and subsoil contained enough sand to facilitate root excavation; because of the absence of perennial weeds; and, especially, because of the uniformity of the soil. A plot 200 feet long and 75 feet wide was located at the foot of a long slope facing southeastward. It had previously been cropped to sweet corn, the size of the stalks and the yield indicating a fairly high degree of fertility.

SOIL

The soil is classified as Wabash silt loam (colluvial phase). It revealed a buried profile as is not infrequently the case in similar soils adjacent to uplands (Weaver, Hougen, and Weldon, 1935). The surface 18 inches consisted of a dark-brown sandy loam. It was darker in color in the first 6 inches, but rather uniform throughout. The second 6 inches was mottled with a considerable quantity of light colored sand which added a grayish tone. The soil was very friable and easily penetrated by roots.

At 18 inches depth there occurred the top of the former surface soil. It was very dark brown or black in color. Its excellent granular structure and apparent high humus content showed conclusively that it was at one time the surface soil. This original "A" horizon contained distinctly more clay than the soil above. It was 14 inches thick.

A gradual transition to the "B" horizon occurred at a depth of 32 inches. Here the soil was yellowish-brown in color, of higher clay content, and less friable than the layer immediately above. It was not so thoroughly penetrated by roots. When moist, it was easily excavated since it contained enough sand to give it a good structure.

The transition to the "C" horizon or massive layer was rather gradual. The massive layer became clearly apparent at about 48 inches. Here the soil was of reddish brown or yellowish brown color and very friable. It contained less clay and more sand and was much more readily removed than the layer above. It was well drained, and occupied by numerous roots. There were some streaks and mottling with iron. No lime concretions were in evidence. The massive layer extended deeply without much change.

The hygroscopic coefficient of the surface 4 inches was 10.6 per cent; that of the 4 to 12 inch depth, 11.1. Those of the second, third, and fourth feet were 11.3, 8.7, and 8.6 per cent respectively. Hygroscopic coefficients of the first three feet of the massive layer were somewhat similar, varying between 8.8 and 9.9 per cent. The surface layer was acid, pH 4.9, and that of the 4 to 12 inch depth slightly less so, pH 5.2. The second, third, and fourth feet gave pH values of 5.9, 6.0, and 6.0, respectively. Acidity decreased with depth, from pH 5.8 in the sixth foot to 6.4 in the eighth.

GENERAL CONDITIONS FOR GROWTH

The mean annual precipitation at Lincoln over a period of 56 years is 27.8 inches. Approximately 79 per cent of this falls as rain during the months of April to September inclusive. Although the rains occur largely as thundershowers with heavy precipitation falling during a short period of time, yet because of the nearly level topography and sandy nature of the soil in the experimental plots, there was no run-off. Periods of drought extending over two or more weeks are common. Average day air temperatures sometimes reach 90°F. but are more usually between 75° and 85°F. Average day humidities vary between 50 and 80 per cent during years of greater rainfall but fall frequently to 40 to 50 per cent during drier years. Wind movement is fairly constant and often high; about 72 per cent of the summer days are entirely clear; and evaporation is high, often averaging 30 cc. daily (Weaver and Himmel, 1931).

The growing season of 1933 was marked by a very dry spring (April and May), although this was preceded by abundant rains in March. Rainfall during June was also below normal; temperatures were extremely high, and the humidity unusually low. Well distributed rains occurred during July, accompanied by moderate temperature and humidity. Drought occurred during the first half of August, resulting in the exhaustion of soil moisture and the ripening of the Sudan grass.

PREPARATION OF SOIL—PLAN OF PLOTS

The cornstalks with the attached coarser roots were removed from the field, which was otherwise free of weeds or other litter. The field was then disked and repeatedly harrowed, thus preparing an excellent seed bed. It was then divided into eight major plots, each 75 feet long and 25 feet wide. These are designated, in accordance with the rate of seeding, normal (N), twice normal (2N), and one-half normal (½N) etc., as shown in Figure 1, where it may be observed that all except the 3N and ¼N plots were in duplicate. Each of the major plots was divided into three smaller ones designated respectively in Figure 1 as A, B, and C. Each subplot A was 25 by 40 feet in extent. The central areas in the plots, each of 100 or 200 square feet, were the portions cut to determine yields. Those in subplots A were cut only after the grain had ripened; those in B and C at approximately fortnightly intervals, the former to a height of 6 inches and the latter to a height of 2 inches.

RATE AND METHOD OF SOWING

The entire field was planted to Sudan grass on May 22, 1933. The normal rate of sowing was 22 pounds per acre (Kiesselbach and Anderson, 1925; Aldous and Zahnley, 1931). The 2N plots received twice this amount of

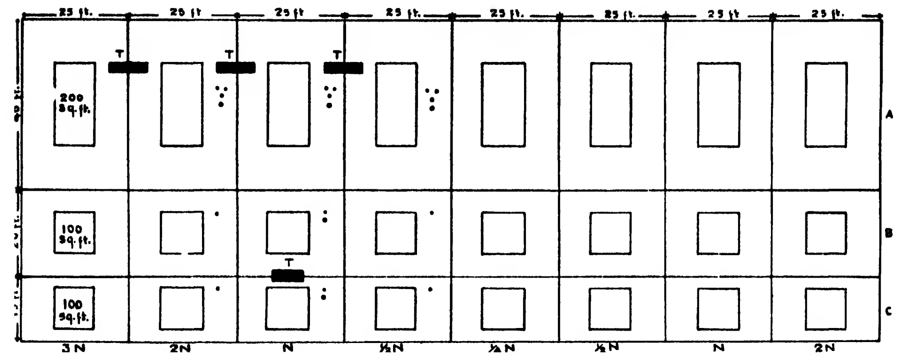

FIG. 1. Plan of experimental plots with subdivisions as described in the text. The trenches excavated in studying roots are indicated by T, and the positions of the insert phytometers by dots.

seed and the other plots the relative amounts designated by their names respectively.

Since repeated experiments indicate that drilling has little advantage over broadcasting, the seeds were sown by the latter method (Hughes and Wilkins, 1926). In order to secure a uniform rate of planting, the lot of seed for each major plot was thoroughly mixed with about 15 pounds of soil. The mixture was then divided into halves. One-half was broadcasted by hand lengthwise of the plot and the other half crosswise. After sowing, the field was harrowed twice. Since the soil was in excellent tilth, this covered the seeds quite uniformly.

METHODS AND PROCEDURE

The rate of growth of the plants under each density of planting was determined by weekly measurements of increase in height of selected plants of average size in each plot. The dry weight of tops was also determined at various intervals. In these determinations 50, and later 25, plants of average size were selected from each plot. Measurements of the dimensions of leaves and area of stems and counts of the number of tillers were made. Dry weight was also determined. The area of the parts above ground was ascertained by means of blue prints and a planimeter. The leaves were cut at the ligule or, if only partly unfolded, where they emerged from the sheath. They were carefully flattened for making the prints. The area of the stems was calculated after measuring the diameter and length. Finally, the plants were cut into pieces of convenient size and dried in an electric oven at 98°C. until they reached a constant weight.

Determinations were made of the relative osmotic pressures of the cell sap of the leaves under different rates of planting. Studies were also made on the anatomical structure of leaves and roots under several different degrees of competition.

Phytometers were used in order to measure directly the water losses during various intervals from unit areas of the plots both under different densities of planting and heights of cutting. They were also used for determining weight and volume of roots and tops. These consisted of containers of three different sizes planted to Sudan grass at the time of seeding the plots. Three had a cross-sectional area of 1 square foot and were 2 feet deep, five had 76 square inches of soil surface when filled and were 2.5 feet deep. Twelve smaller ones, in which the plants were grown for shorter periods, were 54 square inches in area of tops and 1.5 feet deep (Fig. 2). Each container was filled with the soil dug from the hole where it was installed and in such a manner that each six-inch layer of soil occupied the same depth in the con-

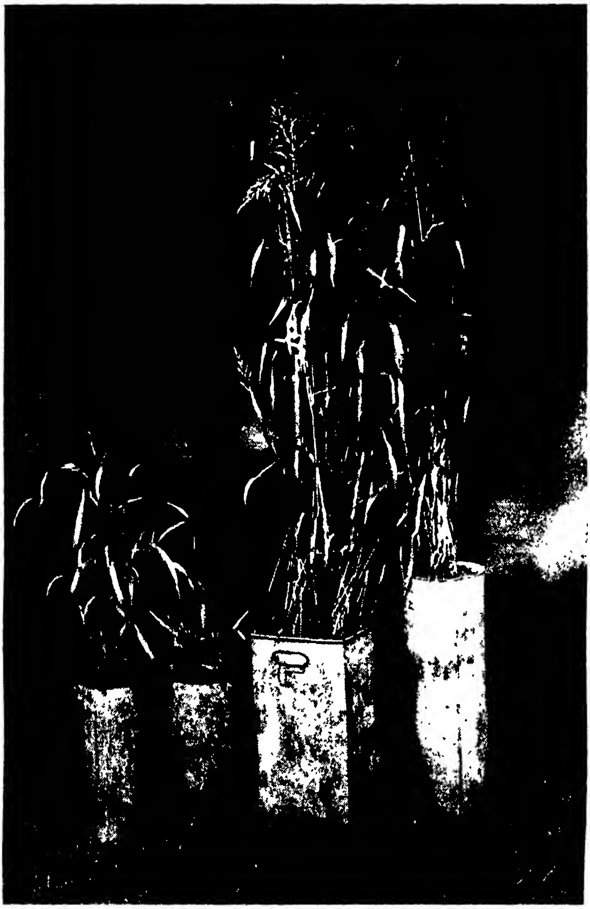

FIG. 2. Types of phytometers used in studies of water loss, and weight and volume of roots under different degrees of competition and clipping. In the large ones on the right, the plants were 6 ft. tall on July 21.

tainer that it had formerly occupied in the field. The tops of the containers were slightly above the soil surface so that they received no run-off water. Each hole was just large enough to receive its container and the container was surrounded by Sudan grass of the regular thickness of planting for that plot. The Sudan grass was sown thickly in the container so as to insure a thick stand and thus permit of thinning to the same density of stand as that of the crop surrounding each container. The locations of the different types of phytometers are shown in Figure 1. Competition was also measured by growing isolated sunflowers in the several plots.

The dry weight and volume of the root systems were determined at several intervals from the plants grown in the containers. This was done because of the difficulty of recovering the entire root system unless enclosed. At the completion of the studies on water loss, the roots were recovered by cutting the container open lengthwise, after placing it in a slanting trough. The soil was washed away with a fine spray of water from a hose and the root systems left almost completely intact. The muddy water was allowed to run through a screen of 2 mm. mesh, upon which the few broken root-ends collected and were recovered. All surface water was removed by pressing the roots repeatedly for a few minutes between blotting paper, and the volume was then determined by immersing them in water contained in a graduated cylinder and ascertaining the volume of the water displaced. This equalled the volume of the roots.

The development of the root system under normal rate of planting was determined at regular intervals by the direct, trench method described by Weaver (1926). At each time of excavation the root systems of several plants, with tops of average size, were exposed and measured. After numerous measurements, a typical root system was selected and drawn to scale. Comparative studies were made on the root development in the thicker and thinner plantings and in the plots that were cut at different heights. Although the same trenches (Fig. 1) were used throughout, they were not only refilled after each excavation but also sufficiently enlarged at the following excavation so that all roots were taken from normal, undisturbed soil.

Soil sampling for water content was done with a Briggs' geotome. Duplicate samples of about 200 grams were secured from the several soil layers to a depth of four feet. Each sample was brought to a constant weight at 110°C. and water content was based on the dry weight of the soil. Soil acidity was determined by the quinhydrone method. Other factor measurements were made as described by Weaver and Clements (1929).

For the sake of clarity, the development of the tops and roots of Sudan grass from seed to maturity, *i.e.*, its life history under the normal rate of planting, will be given first. The effects of competition under different rates of planting will then be discussed. Finally, the behavior of the plants under different heights of cutting will be given.

LIFE HISTORY OF SUDAN GRASS

The large seeds sown on May 22, germinated rapidly in the warm, moist soil, planting having been immediately followed by rain. Numerous shoots appeared above the soil surface after four days.

DEVELOPMENT OF SEEDLINGS

Many small plants were excavated and a representative sample was drawn (Fig. 3A). Although the shoot was only an inch high, the primary root was three inches long. It was about a millimeter in diameter, turgid, white, and had developed no branches.

Three days later the first leaf had attained a length of 2 inches and the second one, although not fully grown, was slightly longer. The spread of the leaves was already 2.5 inches. The primary root was 4.5 inches long, and branch roots of the first order were quite abundant near the surface of the soil. Penetration was nearly vertically downward (Fig. 3B).

Growth continued so rapidly that only four days later, on June 2, a height of 4 inches had been attained. The shoot had 3 leaves, and the fourth was appearing. The longest leaf measured 4 inches. The primary root had extended nearly straight downward to a depth of 9.5 inches. Many branch roots of the first order had developed. Some had extended laterally to a maximum distance of 1.5 inches. A single root system occupied a cylinder of soil 2.5 inches in diameter and 9.5 inches deep (Fig. 3C).

During the following period of 3 days the shoot had unfolded a fourth leaf and the tip of the fifth was over 4 inches long. The roots had made a steady growth. The primary root continued its vertically downward course to a depth of 10.5 inches and long branch roots entended laterally. Short roots of the second order now occurred for the first time. The first root of the secondary root system also appeared on June 5, 14 days after planting. It originated from the lowest node of the shoot. It was 2 mm. thick and well supplied with root hairs.

After three more days of growth, the seedlings were 5.5 inches high; they had 5 or 6 leaves each and a spread of leaves of about 5 inches (Fig. 3E). The first tiller was beginning to develop in the axil of the lowest leaf. The primary root was 13 inches long. Both primary and secondary laterals had made a good growth, and the older portions of the main root had begun to decorticate. The secondary root system had added two new roots, both arising from the lowest node. The oldest was nearly 3 inches long. They penetrated rather vertically downward.

The ability of this crop to withstand high temperatures, low humidities, and severe drought was clearly exhibited during this period. On the afternoon of June 9, for example, the air temperature was 108°F. four feet above the soil surface and 116°F. four inches above the surface. The surface soil

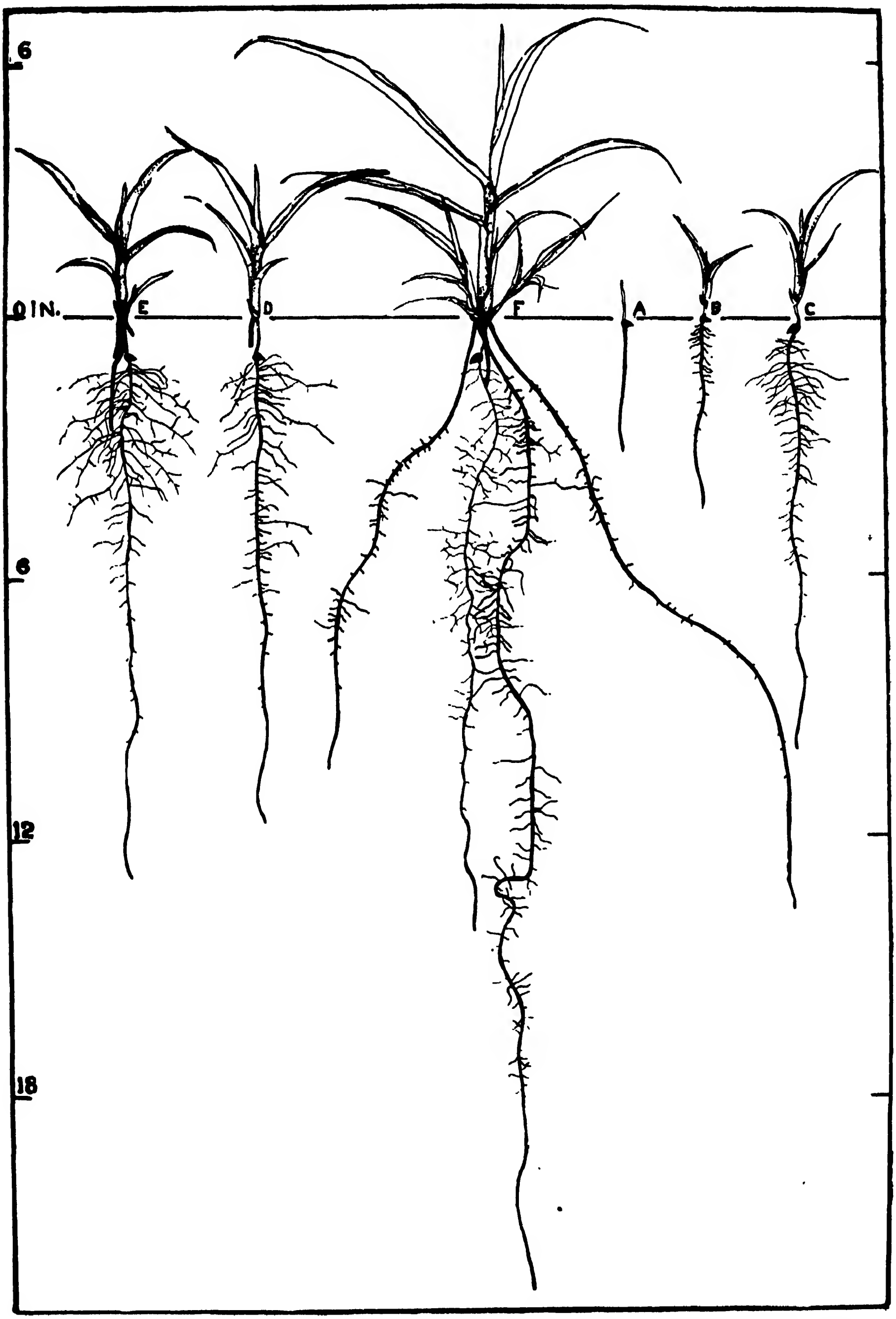

FIG. 3. Seedlings of Sudan grass at the ages of 4, 7, 11, 14, 17, and 21 days respectively. The smallest was excavated on May 26 and the largest on July 12.

had a temperature of 149°F. and the temperature at a depth of 4 inches was 105°F., although it rapidly decreased with depth to 78° at 1 foot. There was no available water in the upper 4 inches of soil, which contained the bulk of the absorbing system. Humidity was only 17 per cent. Although the leaves rolled partly during the hottest part of the day, they recovered at night and growth proceeded steadily.

GROWTH DURING TILLERING

The plants were again examined 4 days later, on June 12. Although the surface soil was quite dry (Table 1) the deeper soil was moist. Atmospheric conditions for growth were favorable and development was rapid. The plants averaged 12 inches in height and had produced three tillers, the oldest about 5 inches tall. The parent plant had 7 leaves and the spread of tops was 11 inches. The leaf area was 14 sq. in. and the dry weight 0.44 gram. The primary root had grown but little, but the secondary root system had made a rapid development. In fact, it exceeded the primary root in depth (Fig. 3F). It consisted of 3 main roots, 22.5, 16, and 11.5 inches in length respectively, and a very young one only 1.5 inches long. The older roots had numerous branches of the first order which spread horizontally. Their absorbing surface exceeded by far that of the primary root system. A rain of 0.72 inch fell on June 12, and replenished the soil moisture (Table 1).

After another 5-day period (June 17), the plants averaged 15 inches high. They had three well developed tillers with an average height of 7 inches. The

TABLE 1. Water content of soil in the N plot in per cent in excess of hygroscopic coefficient to a depth of four feet, and total rainfall between periods of sampling.

Date	0 to 4 Inches	4 to 12 Inches	1 to 2 Feet	2 to 3 Feet	3 to 4 Feet	Inches rainfall
May..24	9.2	11.7	11.9	14.7	15.9	0.00
29	7.8	11.5	12.2	....	....	0.18
June.. 3	5.1	8.4	9.4	....	....	0.00
8	—1.5	6.7	8.7	....	....	0.00
13	10.5	6.1	8.4	14.2	14.7	0.72
19	—3.7	—0.5	5.7	13.3	....	0.00
24	—5.3	—1.9	4.9	11.6	14.2	0.07
29	—6.1	—1.6	0.9	11.8	14.6	0.00
July.. 5	—3.4	—0.7	1.5	13.0	13.7	1.74
7	13.4	0.4	1.0	8.1	12.2	0.66
12	9.5	—0.1	1.2	5.5	9.9	0.55
17	12.9	5.7	0.6	4.4	9.1	1.83
18	14.0	10.9	0.7	4.3	9.2	1.29
22	13.9	7.6	1.2	4.3	8.4	0.44
27	9.8	6.3	0.6	3.8	8.2	0.87
Aug... 1	4.2	2.4	—0.3	3.6	8.2	0.00
7	—1.3	—0.9	—1.0	2.5	7.9	0.03
12	—2.1	—1.5	—1.4	2.3	7.4	0.55
Hygro. Coeff...	10.6	11.1	11.3	8.7	8.6	Total 8.93

primary root had penetrated to a depth of 27 inches. The secondary root system consisted of 9 roots; the longest was 2.5 feet. Most of the secondary roots ran out obliquely at an angle of about 45° to a depth of almost a foot, and then turned somewhat vertically downward. The older secondary roots were densely covered with branches, especially the first foot near the surface of the soil. The lateral spread of the root system averaged 14 inches (Fig. 4A).

When the plants were 30 days old, on June 21, the shoots had nine leaves each and were 2 feet high. The tops had a spread of 21 inches (Fig. 4B). The leaf area was 52 sq. in. and the dry weight of tops averaged 1.59 grams. The primary root had made little growth in the rapidly drying soil (Table 1) but the secondary root system grew very rapidly. It consisted of 13 main roots, the longest slightly exceeding 3 feet. Some of the roots ran rather horizontally outward, others obliqued downward, all into territory unoccupied by the primary root. All of the secondary roots were profusely branched with laterals averaging about an inch in length. The total spread of the root system was 20 inches.

Maturing and Mature Plants

Further measurements were made 11 days later (July 2), but the roots were not excavated. This had been a period of severe drought. The plants had reached a height of 46 inches and had a dozen widely spreading leaves. The panicles were beginning to appear; no new tillers had been formed. The leaf area had increased from 52 to 104 sq. in., and the dry weight from 1.59 to 5.5 grams. The dry weight of the roots obtained from plants grown in the phytometers averaged 2.0 grams.

The development of both tops and roots was again studied 15 days later, on July 17, when the plants were nearly fully grown. Notwithstanding heavy rains, totaling nearly 3 inches since the last examination, the rapid growth had nearly depleted the soil moisture, especially in the second foot of soil, and considerably reduced that of the third foot. The basal leaves had dried and only 7 green upper leaves remained. The total area of the green leaves was approximately 200 sq. in., and the dry weight of the top had increased to 11.4 grams. The parent plant had 2 very small branches and 5 tillers. Three of the tillers were dead. Only one of the tillers and the main stem bore panicles. That of the parent plant was 10 inches long and 7 inches wide; the grain was in the "milk" stage of development (Fig. 5).

The primary root had penetrated to a depth of 4.25 feet and was well supplied with laterals. The secondary root system consisted of 26 main roots. Six had reached a depth of about 5.5 feet; 10 were 3 to 4 feet long; but the remainder were all still in the surface foot (Fig. 6). All except the younger ones were profusely branched throughout to within 6 inches of their tips. The

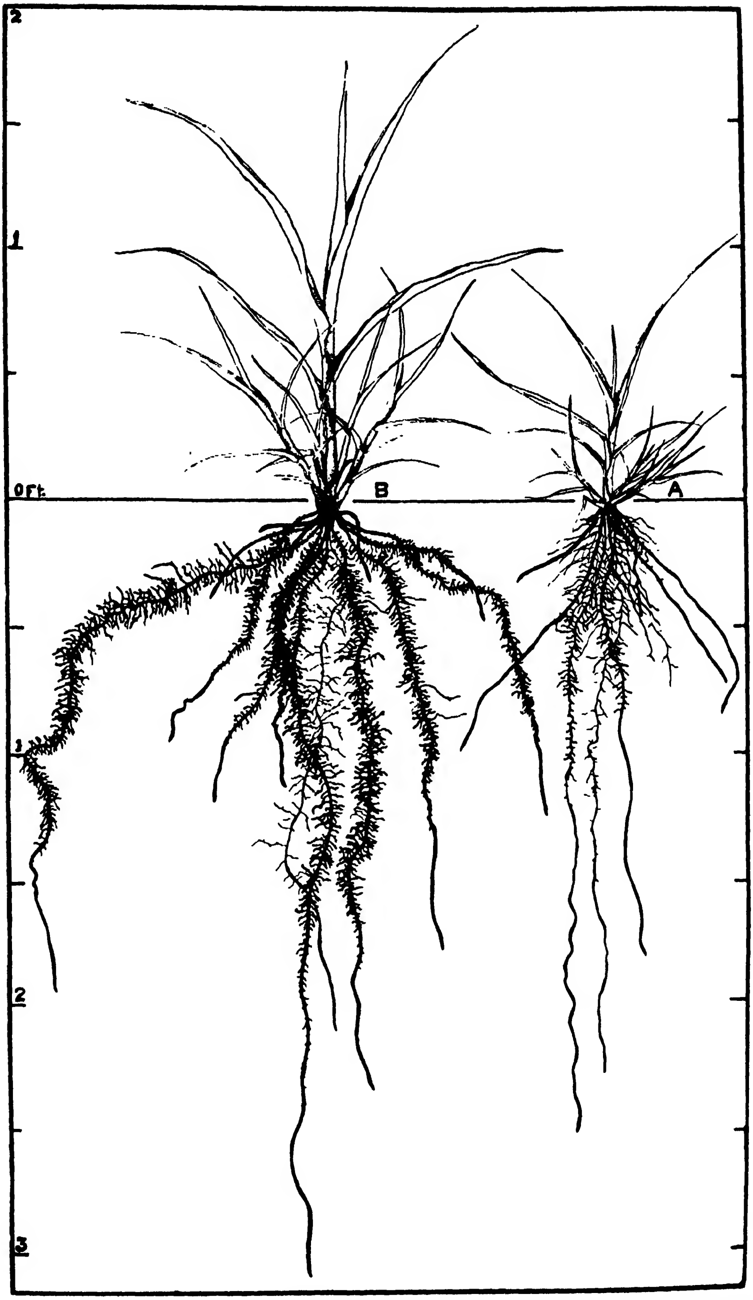

FIG. 4. Development of Sudan grass on June 17 and 21, 26 and 30 days after planting.

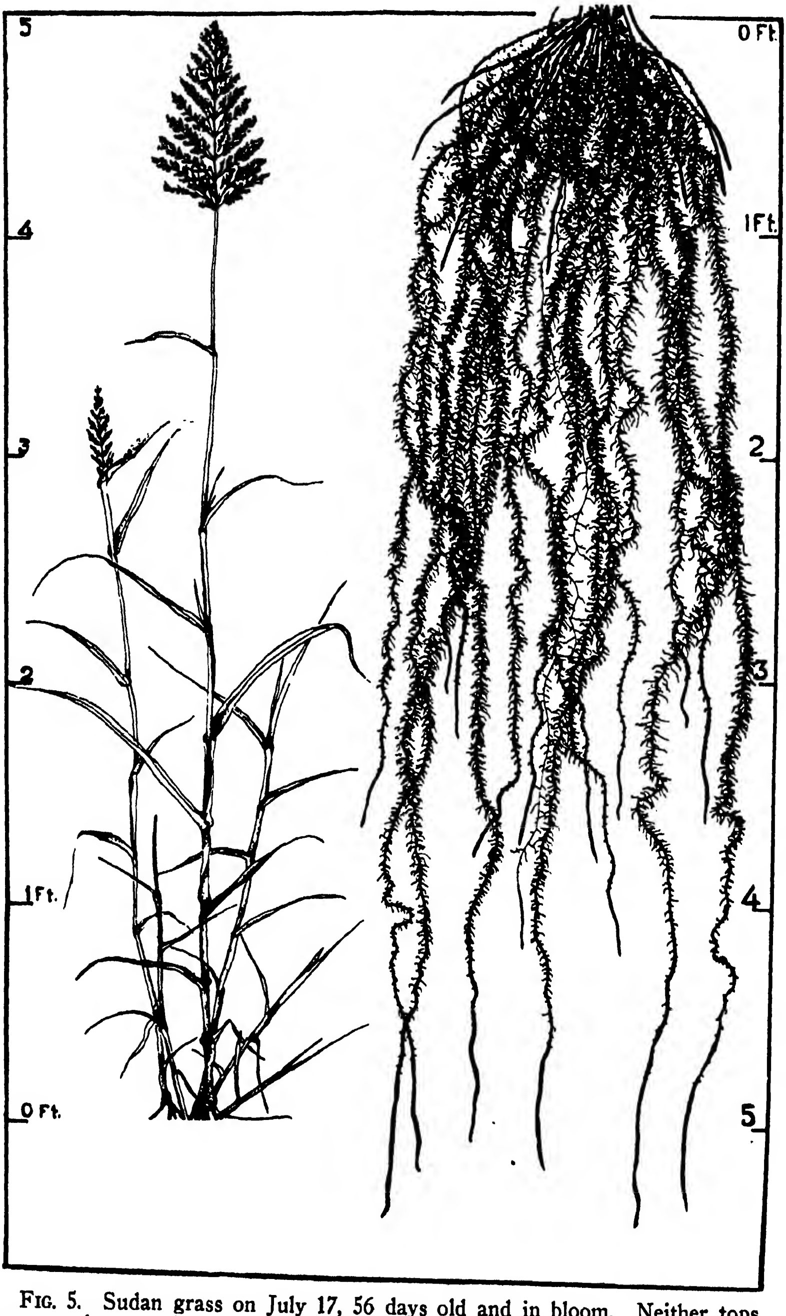

FIG. 5. Sudan grass on July 17, 56 days old and in bloom. Neither tops nor roots have attained their maximum size.

secondary roots at first generally extended obliquely and then turned downward. The whole root system occupied a cylinder of soil 23 inches in diameter and 5.5 feet deep.

The plants were 72 days old on August 2, 17 days after the last examination. Water for growth was exhausted in the second foot, there was only 2 to 4 per cent available in the surface foot, and supplies in the deeper soils had been greatly reduced (Table 1). The shoot had only 6 green leaves although the height was 7 feet. Many of the lower leaves were dry and yellow. The area of the living leaves had scarcely increased. It was 207 sq. in. Only two tillers remained alive, of which one bore a small panicle. The panicle of the parent plant was 12 inches long and 8.7 inches wide. The grain was in the "dough" stage.

FIG. 6. Methods used in excavating roots in the field, although only 56 days old, the Sudan grass had reached a maximum depth of 5.5 feet.

A final study of both tops and roots was made after another 15-day interval, on August 17. The plants were now 87 days old, the seed was ripe, and the crop mature. This development had been hastened by drought. The shoots attained an average height of 7.5 feet. The air dry weight of the grain produced by the parent plant averaged 6 grams. The primary root had penetrated no deeper (4.25 feet) than at the previous excavation 30 days earlier. The secondary root systems consisted of 28 mains roots and their branches. Most of the roots penetrated to about the 4-foot level, but the longest ones to 6.8 feet. The mature root system occupied a volume of soil 2 feet wide and 6.8 feet deep.

Discussion

Sudan grass, introduced into the United States in 1909, has become the most important annual grass for hay. Although it can not be used as a full season pasture grass, since it can not be sown until late in spring and is killed by the first frost, still it is becoming an increasingly important crop for summer pasturage. The stems are coarse but the abundant leaves are rather soft.

Sudan grass is well adapted to drought. When rains came, the seeds germinated promptly and a main root penetrated downward at an average rate of 0.75 inch per day during the first 20 days. At the end of this time the first roots of a very elaborate secondary root system had exceeded the primary root in length. During this period of seedling development, the shoot also made a rapid growth, but it was always exceeded in length by the root system. The general diameter of the root system was blocked out after the first month of growth, and its further development consisted in elongating, branching, and the addition of new roots.

During the second 20-day period root penetration increased to an average of 1 inch per day and new roots were added rapidly. Only at the end of this time, and after tillering had practically ceased, did the length of tops equal the depth of the roots. During the third stage of development, root penetration continued at the rate of 0.8 inch per day, over a period of 47 days. Because of rapid elongation of the shoot and the production of panicles, height of tops exceeded depth of roots throughout this period.

At any time during its growth, this grass can go into a period of semidormancy during extreme drought and revive upon the advent of rains. This probably accounts for the finding of Shevelev (1927) in Russia who states that "during the first month its root system develops faintly." Thus the plant is adapted to drought, first by its rapid germination when water in the surface soil is available, by the rapid development of an excellent absorbing system of great depth and intricate branching which exceeds in extent for a long time that of the tops, and finally by its ability to become dormant and recover after excessive drought.

A mature plant occupied a cylinder of soil 2 feet in diameter and over 6.5 feet deep. There was a single primary root which penetrated to a depth of 4.25 feet, but the secondary root system had 28 main roots. The height of the plant at maturity was about 7 feet. The entire development had been made in slightly less than 3 months.

Because of drought, the increase in area of green leaves was far less than that of the total leaf area. This was due to the dying of the lower leaves as new ones were produced above. Hence, the increase in dry weight of tops occurred at a greater rate than did the area for photosynthesis. Leaf areas during a period of nineteen days during tillering were increased 640 per cent, and dry weight 1155 per cent. Similarly, during the following 32 days the leaf area increased 100 per cent and dry weight of tops 155 per cent (Fig. 7).

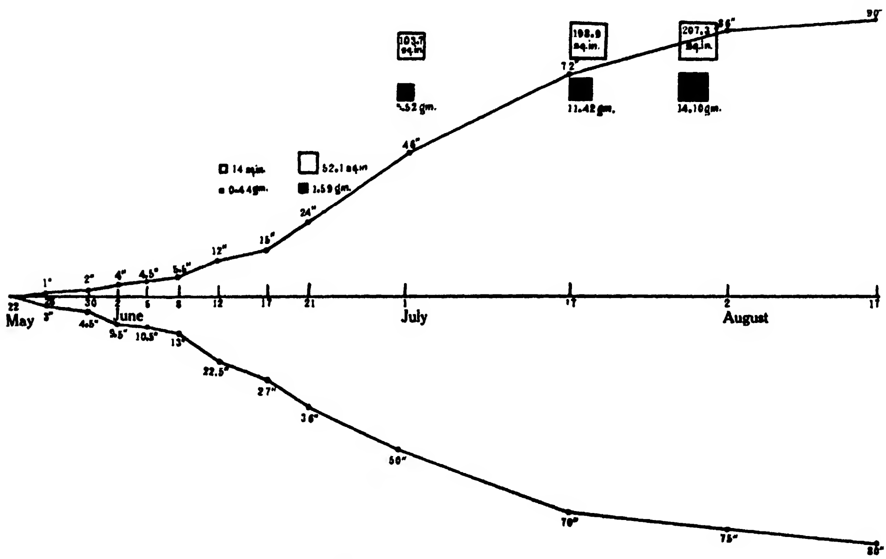

FIG. 7. Relative rate of growth of tops and roots of Sudan grass.

Sudan grass is a heavy consumer of soil moisture. This is due both to its rapid development and to the extensive leaf area resulting from abundant tillering. In addition to using almost 9 inches of rainfall, the crop reduced the original soil moisture practically to the non-available point. Had there been more water available in the upper layers of soil, younger roots could have extended to the deeper layers. These would have more completely exhausted the water in the deeper soil. It seems probable that in addition to the large quantities of water, the crop also made excessive demands on the soil nutrients and thus modified the normal relations of many physical and chemical processes. These reactions deserve special study and until they are understood the use of Sudan grass in crop rotations, especially in dry lands, should be made with caution.

COMPETITION UNDER DIFFERENT RATES OF PLANTING

The seeds germinated promptly and uniformly in all of the plots under the several thicknesses of planting. Conditions for growth were very favorable. Comparisons of the relative development of the plants under each of the several degrees of competition were made at five different intervals. Various measurements of the environmental factors were also made and certain physiological responses determined between these intervals.

Measurements of height indicated that competition had begun by June 9, 18 days after planting, but even on June 12 close observation in the field was necessary to reveal differences in the development of plants.

FIRST EXAMINATION

The plants were first measured on June 12, with the results recorded in Table 2.

TABLE 2. Development of plants under the several degrees of competition on June 12.

Criteria	3N	2N	N	½N	¼N
Average height, cm	25.1	27.3	31.8	32.1	32.7
Average diameter, stem, mm	3.5	4.7	5.3	5.8	5.9
Average number living tillers	2.0	2.2	2.8	3.0	3.3
Average number leaves	5.9	6.2	7.1	7.3	7.5
Average length of fifth leaf, cm	20.2	21.1	18.8	18.1	18.2
Average width leaves, mm	8.9	10.9	10.5	12.3	12.2
Average area, green leaves, sq. in	5.3	5.5	14.0	19.0	19.3
Average area of stem, sq. in	1.6	1.8	2.5	3.4	3.6
Average dry weight, grams	0.23	0.33	0.44	0.63	0.68

The data in Table 2 are from 50 representative plants of average size from each thickness of planting. They show a consistent increase in height and diameter of stems from the thickest to the thinnest planting. The average number of tillers increased from 2 to 3.3, and in accord with this there was a small but consistent increase in the average number of leaves. While there were only slight differences in the length of the leaves, which were more attenuated in the thicker plantings, they increased in diameter from the thickest to the thinnest planting, from about 9 to over 12 mm. Marked differences were found in the average leaf area. Plants in the N field had nearly three times more photosynthetic area than those in the 3N, and the increase from the N to the ¼N was 38 per cent. Smaller but somewhat similar differences occurred in area of the stems. Total dry weight of tops from the thickest to the thinnest planting increased threefold.

A rain on June 12 replenished the water content of the dry surface soil (Table 1). Clear weather prevailed. The mean day temperature varied between 82° and 93°F., and the plants grew rapidly. Before the end of the 9-day period, however, all of the available water had been absorbed from the surface foot and the plants were getting their moisture from the subsoil.

SECOND EXAMINATION

A detailed view of the grass under normal rate of seeding, on June 21, together with one of the small phytometers temporarily elevated before a background, is shown in Figure 8. The plants of the phytometer were in every way comparable to those in the surrounding field. At this time 50 plants were again selected from each plot for measuring. Representative plants, approximately conforming to the average measurements, are shown in Figure 9.

The sequence as regards height and diameter of stems was as before, the plants having approximately doubled in height. All had increased in number of tillers, ranging from 20 per cent in the 3N planting to 145 in the ¼N. The number of leaves increased as before with thinness of stand but, so severe was the competition, the thinner plantings now also had the longest leaves. The width of the leaves was about 15 and 23 mm. in the thickest and thinnest plantings respectively. The photosynthetic area was in the same general sequence as before, that in the 3N plot having increased slightly less than 5 times, and that in the ¼N somewhat more than 5 times. It was 24 and 110 sq. in. respectively. The percentage gains in dry weight were 208, 260, 261, 257, and 390 respectively. The weight of the N plants averaged 1.59 grams.

The weather from June 21 to July 1, when measurements were again made, was very dry until a rain of 1.7 inches fell during the last two days of June. The average day temperatures varied between 85° and 95°F., max-

FIG. 8. Detailed view of plot with normal rate of planting and an insert phytometer, on June 21.

imum temperatures often exceeding 100°F. The average day humidity varied between 35 and 45 per cent. Available water content in the N plot was almost exhausted to a depth of 2 feet, but the deeper soil remained moist.

Comparison of Aerial Environmental Factors

The plants were now about two feet tall and each plot presented a different group of environmental factors. Comparative measurements of light intensity, humidity, evaporation, and transpiration were made in each thickness of planting.

Measurements of light intensities were made near noon on a clear day, June 28, at a height of 6 inches above the soil surface. Clements' photometers were employed and the results were expressed in percentages of full light at meridian. The averages of six readings in each plot from 3N to ¼N respectively, were 23, 27, 44, 47, and 60 per cent.

Humidity 4 inches above the soil surface was measured about noon on a cloudless day, July 3. Cog psychrometers were employed and five separate determinations in each plot averaged. The plants in the N plot were nearly 4 feet tall. The air was most humid in the thickest planting (60 per cent), and the humidity decreased to 54, 50, 48, and 46 per cent, in order in the thinner plantings.

Evaporation was determined by placing Livingston's standardized spherical porous cup atmometers 3 inches above the surface of the soil. Each was provided with a non-absorbing device; the period for evaporation extending from June 27 to July 5. The corrected average daily loss in the 3N plot was 18.6 cc.; it increased to 20.1 cc. in the 2N, and to 24.8 cc. in the N. In the thinner plantings losses of 28.9 cc. and 31.3 cc. were obtained.

FIG. 9. Representative plants showing relative development of Sudan grass on June 21; 3N (left) to ¼N (right).

RESULTS FROM PHYTOMETERS

Water loss from phytometers in the 2N, N, and ½N plots was determined during a dry, hot, rainless period, June 24 to 26. Each phytometer had an area of soil surface of 54 square inches. The phytometers were removed from the field, and the containers freed from any adhering soil. They were then weighed and returned to their respective positions in the field, being entirely surrounded by plants of the same thickness of planting. Since the root systems were confined to a somewhat smaller volume of soil, especially as regards depth, than were those in the field, an equal amount of water had been added to each phytometer to compensate. In every case the plants in the phytometers were similar to those in the surrounding field. The phytometers were again weighed at the end of the experiment. The experiment was repeated with a similar set of phytometers on June 28 to 30. In both cases dry weight of tops and roots and volume of roots were determined. The results are given in Table 3.

TABLE 3. Rate of water loss from insert phytometers from June 24 to 26, and from June 28 to 30, and the relative development of tops and roots.

	June 24 to 26 (54 hrs.)			June 28 to 30 (51 hrs.)		
	2N	N	½N	2N	N	½N
Number plants per phytometer	8	4	2	8	4	2
Total water loss, gm.	936	1250	1148	973	1123	1004
Water loss per plant, 24 hrs., gm.	52	139	255	51	118	211
Average dry weight tops, gm.	1.35	2.73	5.14	2.19	4.05	7.67
Average dry weight roots, gm.	0.98	1.90	3.22	1.04	2.07	3.35
Average vol. roots, cc.	9.7	16.7	33.0	9.3	19.5	35.0

Water loss included both transpiration and surface evaporation. Evaporation from the dry soil surface was very little under the cover afforded by the crop. The daily water loss per plant in the two experiments was fairly uniform in the 2N plot. Cloudy weather on June 29, reduced the loss in the N and ½N plantings 15 and 17 per cent respectively. Average water losses per plant from the 2N plantings were 60 per cent less than from the N. The ½N, however, lost 81 per cent more than those of N rate of planting.

The effects of the increasingly severe competition are reflected not only in the dry weight of tops but also in root development. Average weights of tops were in the ratio of 1:1.9:3.6, and the roots 1:2.0:3.2. The volume of roots of plants from the N plots was about twice that of the 2N but only about one-half as great as the ½N.

COMPARISON OF WATER CONTENT

Water content in excess of the hygroscopic coefficient was determined in several plots on June 24 (Table 4).

TABLE 4. Water content in per cent in excess of the hygroscopic coefficient in the several plots on June 24.

Plot	0 to 4 in.	4 to 12 in.	1 to 2 ft.	2 to 3 ft.	3 to 4 ft.
3N	—5.7	—4.4	—1.3	10.7	15.6
2N	—5.6	—2.8	0.6	10.7	14.4
N	—5.3	—1.9	4.9	11.6	14.2
½N	—2.7	1.2	5.8	12.8	15.6
¼N	—2.0	4.2	9.2	15.3	15.9
Hygro. coeff.	10.6	11.1	11.3	8.7	8.6

Examination of Table 4 shows that water in the shallow soil was reduced by absorption and surface evaporation below the hygroscopic coefficient, but to a smaller degree in the progressively thinner plantings. A similar sequence prevailed in the 4 to 12-inch layer of soil except that here water was available in the ½N and ¼N plots. More available water occurred progressively in the thinner plantings in both the second and third foot. This was the greatest depth of root penetration at this time.

GROWTH OF WEEDS

The severity of competition for the factors in soil and air were not only shown in the development of the Sudan grass but also in the development of weeds. These were naturally most troublesome in the thinner plantings where they were continuously removed; very few developed in the 3N or 2N plots. On June 5, when the Sudan grass was well established, 30 sunflower seeds were planted in each plot, the seeds being spaced widely. Germination was prompt and growth at first was vigorous, but there was no time during the summer when the grass was overtopped by the sunflowers even in the thinnest planting. On July 7, when the sunflowers were 32 days old, their height was determined. It averaged, from the 3N to ¼N plot, 15, 16, 21, 24, and 27 inches respectively. The taller plants also had the thicker stems and the larger leaf surface, defoliation of the lower leaves having occurred in the thicker grass.

THIRD EXAMINATION

Further measurements of the development of Sudan grass were made on July 1. Panicles had begun to appear in the thicker plantings, and especially in the 3N where drought was most severe. Because of the large size, only twenty-five plants were selected from each density of planting for detailed study (Table 5).

The data in Table 5 show that the plants in the thickest plot were shortest and those in the thinnest plot tallest. This was also the sequence at the last examination on June 21. The percentage increase in height, since the last measurements, was 71, 77, 94, 98, and 109 in the 3N to ¼N plots respectively.

TABLE 5. Development of plants under the several degrees of competition on July 1.

Criteria	3N	2N	N	½N	¼N
Average height, cm.	88.2	104.0	115.2	122.0	130.0
Average diameter stem, mm.	5.9	6.8	7.6	8.4	10.8
Average number living tillers	3.1	3.4	4.1	6.4	10.2
Average number leaves	11.4	12.0	12.3	12.8	13.0
Average length of third youngest leaf, cm.	43.5	48.5	51.3	54.2	58.0
Average width leaves, mm.	17.4	20.5	24.2	27.6	32.8
Average area green leaves, sq. in.	40.7	46.1	103.7	270.0	405.0
Average area stem, sq. in.	11.2	12.0	12.8	36.9	96.8
Average dry weight, gm.	2.07	3.28	5.52	11.5	19.47

The stem diameter also increased in the same sequence from 5.9 mm. in the 3N plots to 10.8 in the ¼N. There were more than three times as many tillers per plant in the ¼N plot as in the 3N. Leaves in the thinnest plantings were 25 per cent longer and 47 per cent wider than in the thickest. A very great difference occurred in photosynthetic area; the average for the thickest plantings was only 40.7 sq. in. while that of the thinnest was 405. The percentage increase in the several plots since the second measurement was 70, 67, 99, 323, and 268 respectively. The increase from 3N to ¼N in stem area was almost ninefold, and that of dry weight about 10 times.

The period of July 1 to 17 was marked by more moderate temperatures (average day 83° to 90°F.) and higher average day humidities (40 to 65 per cent). Except very early in this period, water was available at all depths as a result of well distributed rains. It was least plentiful at depths of 2 and 3 feet where maximum absorption occurred (Table 1).

COMPARISON OF WATER CONTENT

The grass in all of the plots was growing rapidly and environmental differences in the several plots were becoming more pronounced. Water content in each of the plots was determined on July 7 (Table 6).

TABLE 6. Water content in per cent in excess of the hygroscopic coefficient in the several plots on July 7.

Plot	0 to 4 in.	4 to 12 in.	1 to 2 ft.	2 to 3 ft.	3 to 4 ft.
3N	10.9	—3.1	—2.8	4.4	12.6
2N	13.1	—1.1	0.1	7.1	12.4
N	13.4	0.4	1.0	8.1	12.2
½N	15.0	1.6	4.7	9.3	15.5
¼N	19.1	3.2	8.7	10.0	15.4

Only enough rain had fallen between June 24 and July 7 to moisten the surface 4 inches of soil. The water content at 4 to 12 inches depth had gradually decreased (cf. Tables 4 and 6). Absorption at deeper levels was taking place vigorously; the water content had fallen in the third foot in all

the plots—in the ¼N from 15.3 to 10 per cent and in the 3N from 10.7 to 4.4 per cent. In the fourth foot, considerable reduction of moisture had also occurred but to a smaller degree than in the third foot. At both of these levels the soil was driest in the 3N plot and progressively more moist to the ¼N plot where the highest water content occurred.

Comparative Root Development

A study of root development was made on July 11 and 12 in the 3N, 2N, N, and ½N plots by means of the trench method (Table 7). The locations of the trenches in the several plots are shown in Figure 1.

Table 7. Root development of Sudan grass under different degrees of competition on July 12.

Plot	Depth, inches	Total spread of roots, inches	Number roots, secondary root system	Working level
3N	66	9	16	Root tips mostly at 2-foot level; many at 4-foot level; a few at 5 feet.
2N	66	14	18	do
N	68	23	27	Root tips D. distributed from first to sixth foot, most abundant at 4-foot level.
½N	70	28	38	Similar to N.

The data in Table 7 show that the roots in the thinner plantings were better developed than those in the thicker ones. Root penetration, spread of roots, and number of roots of the secondary root system were all least in the thickest planting. They gradually increased with thinner plantings, reaching a maximum in the ½N plot. Thus competition underground was least in the thinnest stand and severest in the thickest one.

Several roots of average length and diameter were selected from the 3N, N, and ¼N plots for anatomical study. The object was to determine the effect of competition upon size and structure of the individual root. The roots were all taken in the third foot of soil, on July 11 and 12. They were cut into sections convenient for killing and fixing in chromoacetic acid solution. After embedding in paraffin, cross sections 12 microns thick were cut and stained in safranin and counterstained with fast green. The averages of a large number of measurements are given in Table 8, and representative root sections in Figure 10.

Even causal examination of Figure 10 shows the profound effect of competition upon root structure. Roots from the 3N plot had the smallest total diameter and the smallest diameter of both cortex and stele. Those from the N plot were largest. With a decrease in the density of planting, the ratio of

TABLE 8. Diameter and area of cortex and stele of roots of Sudan grass.

Criteria	3N	N	¼N
Diameter of root, microns	844	1242	1772
Width of one side of cortex, microns	190	290	426
Diameter of stele, microns	464	662	920
Cross-sectional area of root, sq. mm.	0.550	1.211	2.465
Area of cortex, sq. mm.	0.390	0.867	1.801
Area of stele, sq. mm.	0.160	0.344	0.664
Ratio of area of stele to area of cortex	1:2.4	1:2.5	1:2.7

the area of stele to the area of cortex gradually increased. Stated conversely, the area of the cortex was smaller in proportion to the area of the stele as the density of planting increased. This reduction in the size of both cortex and stele resulted from reduction in the size of the individual cells, rather than from a decrease in their number.

Comparison of Structure of Leaves

Representative leaf materials were collected in the 3N, N, and ¼N plots on July 17, when the plants were nearly fully grown. The leaves were taken from the parent plant (not the tillers) at a height of 18 inches from the soil

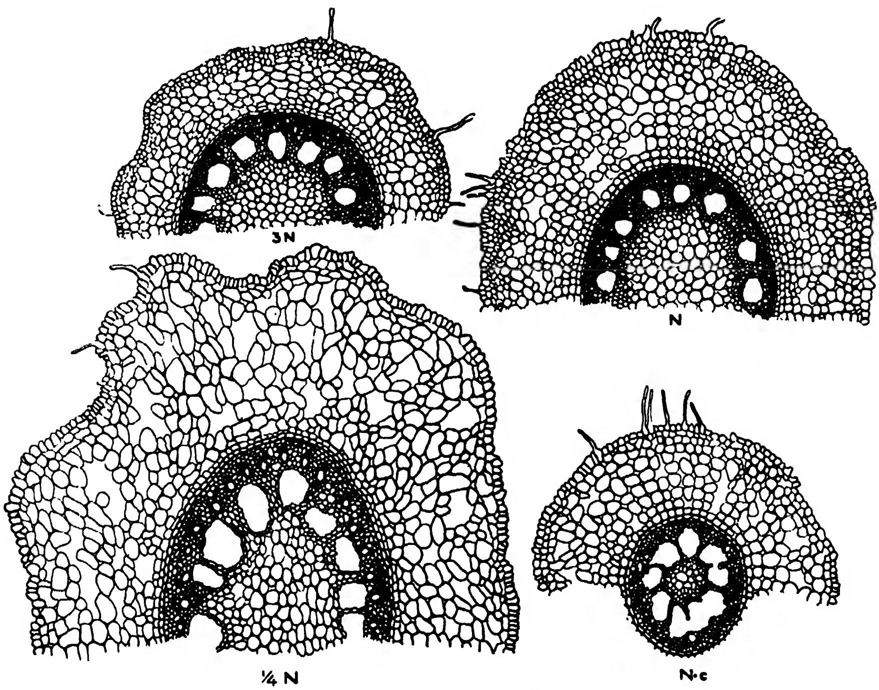

FIG. 10. Cross sections of representative roots taken at a depth of 3 to 4 feet in the several plots on July 12. Also (N-c) a root section from the N plot where the tops were repeatedly cut to a height of 2 inches.

surface. These leaves had received the full impact of the factors of competition for a considerable period of time. Sections 5 mm. square were cut from the blade of the leaf 20 cm. from the ligule and half way between the midrib and the outer edge. They were treated as were the root materials, the cross sections being 10 microns thick. After extended measurements the sections in Figure 11 were selected as representative.

The leaves from the 3N plot were only 103 microns in thickness, those from the N 125, and those from the ¼N 143. The bundles were both larger and farther apart in the thinner plantings, the average distance being 35, 42, and 51 microns respectively. In general, the effects of competition as exhibited by leaf structure in smaller size, closeness of veining, and small compacted cells were those of drought.

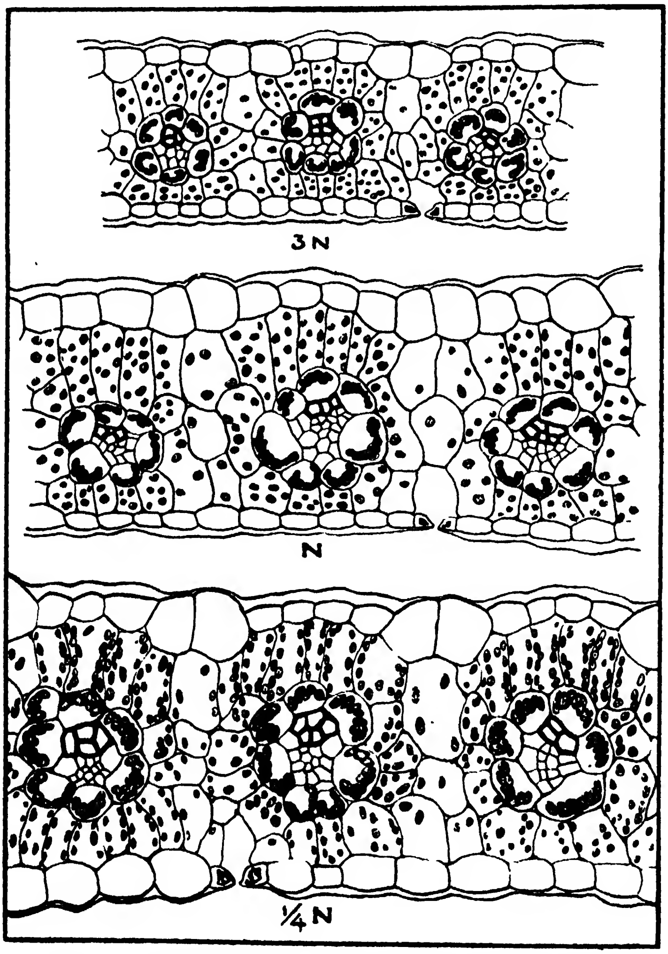

FIG. 11. Representative cross sections of leaves of Sudan grass from the several plots on July 17.

RESULTS FROM PHYTOMETERS

Water loss, from the large phytometers, was determined for a third time on July 15 to 21. Each had a depth of 2.5 feet and an area of soil surface of 76 sq. in. The plants in the large phytometers were about 6 feet tall and had a total photosynthetic area of approximately 200 sq. in. (Fig. 2). The weather was mostly sunny with moderate temperatures but the water losses were relatively high.

TABLE 9. Rate of water loss from phytometers from July 15 to 21, and relative development of tops and roots.

Criteria	2N	N	½N
Number of plants per phytometer	22	9	5
Total water loss, grams	11,560	9,002	8,430
Water loss per plant, 24 hrs., grams	87.6	166.7	281.0
Average dry weight tops, grams	8.0	12.0	38.3
Average dry weight roots, grams	5.3	7.5	18.2
Average vol. roots, cc	22.8	35.0	100.2

Table 9 shows that for a given soil area the total water loss in the 2N plot was greatest and that in the ½N was least. This resulted from the greater number of plants per unit area in the 2N planting. The amount of water lost per plant was greatest in the ½N plot where the plants were fewest but largest. The loss per plant in the 2N plot was 48 per cent less than from the N, but the plants in the ½N plot lost 68 per cent more. The increase of dry weight of tops from 8 to 12 and then to 38 gm. was marked, but scarcely more so than the dry weight and volume of the roots under the different densities of planting. The ratios of dry weight of roots to tops in the 2N, N, and ½N plants were 1 to 1.5; 1 to 1.6; and 1 to 2.1 respectively. Thus the roots had suffered a relatively smaller decrease than the tops, a fact that may be attributed to the greater development of roots in the thicker plantings as a result of the drier soil.

FOURTH EXAMINATION

The development of Sudan grass in the several plots was again determined on July 17, after a period of 17 days (Fig. 12). The panicles had developed rapidly beginning July 1 and were mostly unfolded after 7 to 10 days. Their development was most rapid in the 3N plot but decreased regularly with wider spacing, being longest delayed in the ¼N plot.

The plants of the thickest plantings were smallest in every way; there was a progressive increase in all measurements of size and weight with decreased thickness of stand, the ¼N plantings showing the greatest development. The average area of green leaves, for example, increased from the 3N to the ¼N planting in the ratio of 1:1.7:4.1:7.9:13.3. This dwarfing of stature is at-

FIG. 12. Representative plants showing development of Sudan grass in the 3N (left), 2N, N, ½N, and ¼N (right) plots on July 17.

tributed directly to the decrease in light and water, and probably in part to nutrients.

During the next interval, July 17 to August 2, average day temperatures were about 85°F. The average day humidity was 58 to 72 per cent. Two heavy showers maintained a supply of water in the surface foot of soil, but the deeper soils were gradually being depleted of their moisture except the fourth foot (Table 1).

COMPARISON OF AERIAL ENVIRONMENTAL FACTORS

At this time the plants in the N plots were about 6 feet tall. Comparative measurements of light intensity, humidity, and evaporation were made in each thickness of planting.

The average of six readings of light intensity taken at a height of 6 inches above the soil, in the 3N to ¼N plots respectively, were 11, 13, 25, 27, and 32 per cent. The light intensities at this time were only about half as great as those from similar readings taken 23 days earlier when they were, in the above sequence, 23, 27, 44, 47, and 60 per cent.

Humidities on July 19, 4 inches above the soil surface were 77, 74, 69, 69, and 66 per cent in the 3N to ¼N plot respectively.

RELATIVE GROWTH OF SUNFLOWERS

A second measurement of the development of the sunflowers was made on July 28, 3 weeks after the first. All of the plants in the 3N plots had succumbed (Fig. 13).

The increasingly greater development of all parts of the plants with an increase in water and light, as the Sudan grass became thinner, shows clearly the harmful effects of competition upon the individual. The height increased gradually with reduced competition from 41 to 64 inches, the diameter of stem from 6 to 25 mm., the number of green leaves from 7 to 24, and the total leaf area from 2.42 to 112.08 sq. dm. respectively.

FIG. 13. Sunflowers of average size from the 2N (left), N, ½N, and ¼N (right) plots, respectively. The largest is 64 inches high.

The dense shade was unfavorable to chlorophyll development and the sunflowers in the thicker plantings were yellowish green in color. This was probably aggravated by a shortage of nitrogen (cf. Clements, Weaver, and Hanson, 1929). In the 2N plots all but the top leaves were dead. A determination of the starch content of the leaves was made at the end of a clear day. The leaves from the several plots were all selected at the same height—that of the living leaves of the sunflowers in the 2N plot. Sach's iodine test revealed the fact that the plants in the 2N plots were making very little starch, but the amount rapidly increased with the more favorable conditions in the thinner plantings. From the standpoint of weed control, the competitive effects of the Sudan grass are clearly beneficial.

Osmotic Pressure

A sufficient quantity of leaves of Sudan grass for triplicate determinations of the osmotic pressure of the sap was collected at 4 o'clock on the afternoon of July 27. Only leaves of parent plants at a height of 3.5 feet from the ground were selected in each of the several plots. They were frozen for 24 hours in an ice-salt mixture after which the sap was expressed under pressure of 10,000 pounds by means of a Carver press. Freezing-point determinations were then made and the results were expressed in atmospheres by referring to the Gortner and Harris, (1914) table of osmotic pressures. The osmotic pressures increased with decreased thickness of planting as follows: 10.6, 11.9, 12.8, 13.0 to 14.2 atmospheres respectively. Since water was plentiful, at least in the surface foot and in the deep soil (Table 1), the response of the plants as recorded in differences in osmotic pressure seemed to be correlated with differences in the light intensities and consequently the ability to manufacture sugars. Similar determinations in the N plot when the plants were but 18 days old gave an osmotic pressure of 17.1 A., but this was at a time when water content in the surface soil was low, temperature extremely high, and the air very dry.

Fifth Examination

When the grain was beginning to ripen on August 2, 16 days after the last examination, plants were again selected and the usual measurements obtained. At this time the crop was 72 days old (Table 10).

Because of the production of panicles, all of the plants had gained somewhat in height. The increases in the several plots from 3N to ¼N were 10, 11, 18, 21, and 17 per cent respectively. The 3N and 2N showed decreases of 7 and 14 per cent in their area of green leaves, but the N, ½N, and ¼N plots had made gains of 4, 14, and 9.3 per cent during the 16 days. Gains in dry weight occurred in all of the plots. They were, in sequence, from the 3N to ¼N, 15, 17, 24, 63, and 43 per cent.

TABLE 10. Development of plants under the several degrees of competition on August 2.

Criteria	3N	2N	N	½N	¼N
Average height, cm.	187.0	199.2	215.0	230.0	240.0
Average diameter stem, mm.	3.7	4.6	5.7	6.7	9.0
Average number living tillers.	0.5	1.2	2.3	5.3	8.0
Average number living leaves.	4.0	4.9	5.5	6.0	6.0
Average length of third youngest leaf, cm.	45.5	49.7	56.0	56.4	59.4
Average width leaves, mm.	21.5	23.9	25.9	31.0	38.0
Average area green leaves, sq. in.	44.3	72.9	207.3	428.1	692.3
Average area stem, sq. in.	21.3	24.3	40.1	99.0	250.0
Average dry weight, grams.	8.39	9.84	14.10	53.00	109.99

From this time until harvest, on August 17, somewhat lower temperatures prevailed. A rain of 0.55 inch on August 8 was again followed by dry weather. The dry air caused high transpiration losses and the demands of the crop for water exceeded the supply, except in the deeper soil (Table 1).

COMPARATIVE ROOT DEVELOPMENT

The final study of root growth was made on August 17 and 18 when the plants were harvested. Depths of penetration in the 3N, 2N, N, and ½N plots were 74, 78, 82, and 90 inches and the total spread of roots 9.6, 16, 24, and 32 inches. Thus the root system had been dwarfed somewhat in proportion to the tops. Marked differences were also found in the number of roots of the secondary root system. They were as follows: 17, 19, 28, and 44. In the thickest planting, many of the secondary roots ended in the second foot of soil. But with decreased competition and increased available water a larger number of the roots extended deeper.

MATURE PLANTS

The crop matured rapidly during the second week in August. Even the plants in the ¼N plots were drying, and those in the thickest plantings were very dry.

PRODUCTION OF BRANCHES AND PANICLES

Previous to harvesting the crop, on Aug. 17, the degree of branching of the parent plants above ground was ascertained in the several plots. The average number of branches increased with wider spacing of the plants as follows: 0.2, 1.2, 1.6, 2.8, and 3.2.

The number of panicles per plant varied greatly in the several plots. In the 3N and 2N plots competition was so severe that the parent plants alone produced seed. In the N plots an average of 2 panicles was produced, 4 in the ½N, and 8 in the ¼N.

Fifty panicles were selected from parent plants in each plot and the average length and width ascertained as well as the dry weight of the grain (Fig. 14 and Table 11).

TABLE 11. Development of the panicles of Sudan grass from the several plots on August 18.

Criteria	3N	2N	N	½N	¼N
Length of panicle, cm	25.3	28.2	30.2	33.7	37.5
Width of panicle, m	14.9	22.5	25.9	28.1	31.5
Air dry weight of grain, gm	3.62	4.07	6.15	9.55	13.87

Table 11 reveals a direct decrease in the length and width of the panicle with an increased rate of planting. The decrease in dry weight of grain, however, was even more pronounced than that of the panicle. While the panicles decreased 33 per cent in length and 52 per cent in width from the ¼N to 3N, the decrease in yield of grain per panicle was 73 per cent.

YIELDS

In harvesting the crop, it was cut at a height of 2 inches above the surface of the soil. To avoid border effects, only 200 square feet from the middle of each plot was used (Hulbert, Mitchels, and Burkart, 1931). The few weeds that persisted were excluded. After drying for a single day in the field, and before shattering of the seed occurred, the plants were removed to the laboratories where they were thoroughly air dried and then weighed. The yield was greatest (18,786 gm.) from the N plot and least (13,582 gm.) from the ¼N. The next lowest yield (16,530 gm.) occurred in the ½N plot. Thus decreasing the number of plants by ½ reduced the yield only 12 per cent, while a decrease in seeding to ¼ reduced it by 27 per cent. Conversely, doubling the rate of sowing decreased the yield (2N, 18,548 gm.) only 1.0

FIG. 14. Representative panicles from the 3N (left), 2N, N, ½N, and ¼N (right) plots. The largest is about 15 inches long.

per cent, and tripling the amount of seed reduced it (3N, 17,606 gm.) 6 per cent.

The yields per acre were, in order of increasing thickness of planting, 3.25, 3.96, 4.50, 4.44, and 4.22 tons respectively.

DISCUSSION

Clements, Weaver, and Hanson (1929) state that "two plants do not compete as long as the water content and nutrients, the heat and light are in excess of the needs of both. The moment, however, that the roots of one enter the area from which the other draws its water supply, or the foliage of one begins to overshade the leaves of the other, the reaction of the former modifies unfavorably the factors controlling the latter, and competition is at once initiated." The intensity of competition is directly correlated with the degree of development of the different organs of the plants—stems, leaves, and roots. The same investigators state that "the outcome as indicated by the number, size, and form of the plants concerned is a good measure of the intensity of competition." Also that the "effect of competition finds expression in the functions, structure, or form of the individual or of the community."

The degree of competition for water, light, and probably for nutrients as well was clearly illustrated by the results obtained from Sudan grass grown under the five different rates of planting. The first panel in Figure 15 shows the relative heights of the plants in the several plots at various stages of development. Differences in height were not marked, except the 3N planting, until July 1, at the time of stem elongation when competition for light was severe. The more crowded the plants the less able were they to secure sufficient materials to develop as greatly in height as plants in the less crowded, adjoining plot. Thus throughout their growth and at maturity the height increased with thinness of stand.

Competition was not alone for light but especially for water. Available water was always least in amount in the 3N plot and greatest in the ¼N. Thus there existed a direct correlation between the height of shoot and water content. This is explained by the findings of Weaver and Clements (1929), "when the soil is very dry, root development is greatly retarded or even ceases, and the above ground parts are consequently dwarfed."

During the first 5 weeks of growth the reduction of roots in the thicker plantings was nearly in proportion to that of tops. But later the roots showed a greater development than the tops in response to the drying soil and great need for increasing supplies of water.

The diameters of the stems increased regularly with thinness of planting. The maximum, attained on July 1, was 5.9 mm. in the 3N plot and 10.8 in

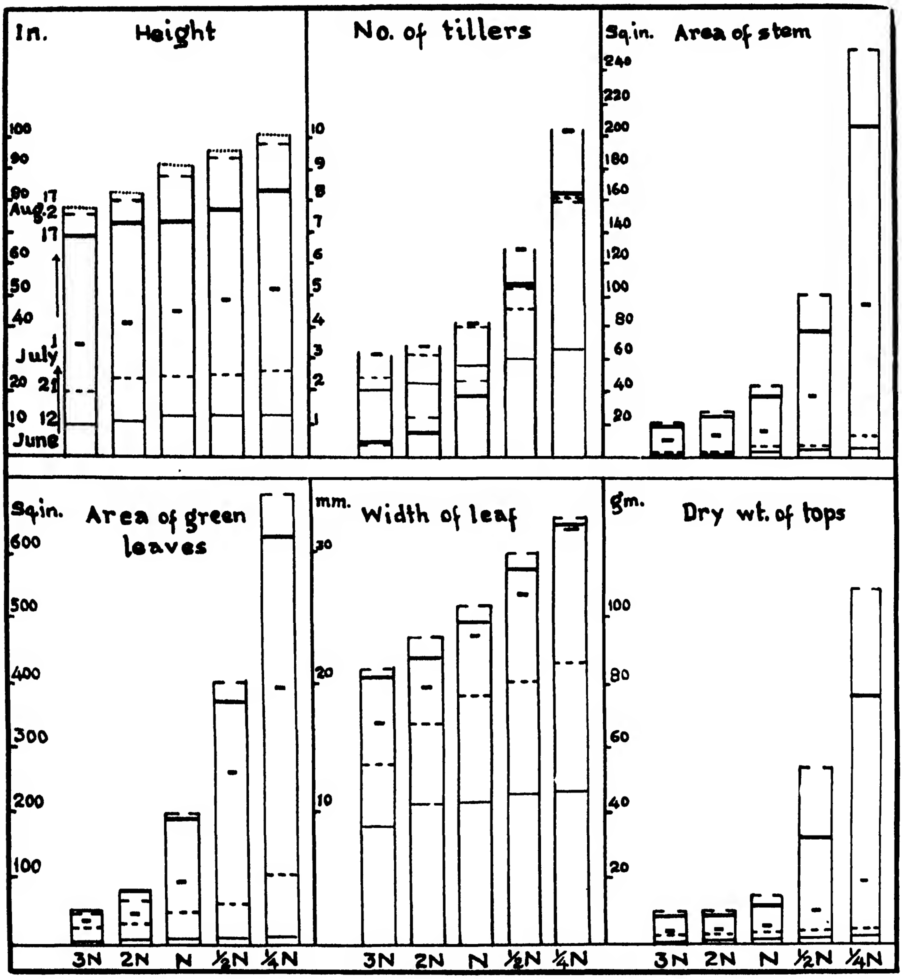

FIG. 15. Relative development of Sudan grass under the different thicknesses of planting.

the ¼N. From thence to maturity, with the drying of the bases and maturing of the plants, there was a steady decrease.

The number of tillers produced from the several plots increased with thinness of planting. The maximum number of living tillers occurred when the plants were 40 days old on July 1. In the sequence of thinness of planting, they were 3, 3, 4, 6, and 10 respectively. The number of living tillers decreased from this time until harvest. This was due to dryness of the soil and partly to insufficient light reaching these new shoots, especially in the thicker plantings.

The differences in the area of the stems from the several plots were far more pronounced than the differences in height. There was a direct correla-

tion between area of stem and density of planting. The increase in the area of stems from 3N to ¼N at maturity was more than twelvefold.

The length of the leaves was greatest in the thinnest planting and the width of the leaves also increased with fewer plants per unit area. Likewise the relative area of green leaves and dry weight of tops from the several plots showed the same trend of behavior. The total leaf area per square meter (10.7 sq. ft.) of soil on June 12 was greatest in the 3N (13.5 sq. ft.) and diminished somewhat regularly to 2.5 sq. ft. in the ¼N. The decrease amounted to 81 per cent.

By June 21, the leaf area in the 3N plot had increased over 4 times, but that in the ¼N nearly 6 times. Assuming that no plants had died by July 1, the leaf area per square meter of the 3N plot was slightly less than doubled (104 sq. ft.) while that in the ¼N had increased almost 4 times (47.7 sq. ft.). The thinnest planting thus had nearly 45 per cent as great a leaf area as the thickest, although it had only 5.2 per cent as many plants. With the great increase of tillers in the thinner planting and their death in the thicker ones, it seems certain that the final leaf area in the ¼N greatly exceeded that of the 3N. Conditions in the other plantings were intermediate.

The average green leaf area per plant was determined for each plot by adding the areas obtained at each of the five examinations and dividing by 5. From these data and the average dry weight per plant on August 2, the dry weight in grams produced per square inch of green leaf area was determined. This was, from the 3N to ¼N plantings, 0.26, 0.20, 0.12, 0.22, and 0.29 gram respectively.

Thus it appears that the well lighted and well watered plants in the ¼N plots were most efficient, and that there was a marked decrease with thickness of planting until the N plot was reached. With a reduction of the green leaf area in the thicker plantings, due to the death of the leaves to near the top of the stems, the efficiency of the remaining younger and better lighted leaves increased. This viewpoint is supported by a study of relative production of dry matter in relation to green leaf area at the time of each of the five examinations. Except during the extreme drought of June, the same sequence was determined in every case.

The water loss, in grams per square inch of green leaf area per day, was greater in the ½N and less in the 2N than in the normal planting during the seedling stage (June 21). The values were 1.8, 3.1, and 3.7 from thicker to thinner plantings. But during the stage of elongation (July 1) the losses were 1.0, 1.1, and 0.8. At maturity, when the plant had received the full impact of drought, losses were greatest in the thickest or most xeric plot and least in the thinnest or most mesic one. The losses were 1.0, 0.8, and 0.7 gram, respectively. This is in accord with the theory of xerophytism as proposed by Maximov (1931).

Results of anatomical study of leaf sections from 3N, N, and ¼N plots reveal the fact that the leaves were thinnest in 3N, and thickest in ¼N. These findings are supported by Weaver and Clements (1929) who state that "the thin leaves present an increased surface in proportion to tissue involved, for the reception of diffuse light." The much smaller area of green leaves and the smaller dry weight of the individual plants in the 3N plot than in the thinner planting were due to a combination of low light intensity and reduced water supply. Brenchley (1919) states that "the decrease in light caused by overcrowding is a most potent factor in competition even when an abundance of food supply and water is presented to each individual plant." This is in accord with the results of Clements, Weaver, and Hanson (1929) that "with light intensity reduced five times, the leaf area was decreased a third, and the dry weight three times in *Helianthus* and *Triticum.*" They state further that "the amount of photosynthate for the 'thins' was 50 per cent larger than for the 'thicks,' the sequence being in agreement with that of density and light values."

Considering the greatest yield, which occurred in the N plot, as 100 per cent, it was reduced 6 per cent by tripling the rate of planting but 27 per cent by decreasing the rate to one-fourth. Thus it appears that under excessive competition more forage was produced than where the plants were too widely spaced. Stated in terms of factors of water and light, it seems clear that the thickest plantings utilized all that were available while in the thinnest plantings, even after maximum tillering, both water and light were often in excess of the demands. They were less so in the ½N where the yield was reduced only 12 per cent; yields in the 2N were reduced only 1 per cent. Thus as stated by Brenchley (1919) "it is generally recognized that up to a certain point, it is profitable to give growing crops plenty of room, but beyond this limit the total yield is apt to fall off."

Had yield of grain been used as the criterion the percentages would probably have been different, but the same general principles would have held. Kiesselbach and Anderson (1925) found that during a period of three years, when Sudan grass was seeded at 10, 20, 40, and 80 pounds per acre at Lincoln, Nebraska, the weight of 100 stalks averaged 1.46, 1.14, 0.94, and 0.72 pounds, respectively. The relative diameters of the stems at the base were, in the same sequence, 0.17, 0.16, 0.14, and 0.11 inch. Chemical analysis showed that the grass did not differ materially in composition even though the coarseness of the forage was decidedly reduced by closer spacing. The yields they obtained from upland soil near Lincoln were very similar to those in this experiment. They varied somewhat with the stage of cutting, from 3.26 tons per acre when cut as the first heads were appearing to 5.04 tons when mature.

Each thickness of planting presented a different set of environmental factors. In the thicker plantings, the surface of the soil was fully covered with

leaves and the loss of water through surface evaporation was low. The relative humidity was fairly high due to the fact that the moisture laden air surrounding the plants was not so rapidly changed by wind movement as was that in the thinner plantings. This environment tended to reduce transpiration. But the large number of plants per unit area of soil (324 per square meter in the 3N as against 17 in the ¼N plot) far more than overshadowed these conditions and resulted in total water losses increasing directly in proportion to thickness of sowing. Phytometers were very useful in measuring these losses directly and quantitatively.

EFFECTS OF CUTTING ON SUDAN GRASS

Sudan grass is frequently used in temporary pastures since it grows well during midsummer when bluegrass and certain other pasture grasses do not thrive. In these experiments one strip 15 feet wide and another 20 feet wide extended at right angles across all of the major plots with different thickness of planting. Plants in the narrower strip were cut at a height of 2 inches and those in the wider one at 6 inches height at six different times throughout the summer (Fig. 1). The purpose was to simulate grazing and thus study the behavior and yields of the plants cut 2 and 6 inches high. While all the plots were cut on the same days, the intervals between cuttings were determined by the growth of the plants. In order to avoid the so called "border effects" (Arny and Hayes, 1918; Kiesselbach, 1919), the yields from only the central 100 square feet of each plot were determined, although the whole plot was cut uniformly and the forage removed. After clipping the entire plot at the proper height, by means of a grass shears, the yields from this central portion were carefully gathered, air dried, and weighed. The last cutting was made on August 18, at the time when the larger, unclipped plots were also harvested. This permitted of a comparison between the sums of the partial yields from each clipped plot with the total yield from the plots where the plants grew undisturbed.

FIRST CUTTING

The first cutting was made on June 22 when the plants in the N plot were 24 inches tall. At this time only, the higher cutting was made at the 9-inch level. Weeds were suppressed in the thicker plantings by the competition of the Sudan grass. Among the more widely spaced plants, they were regularly removed by pulling. Hence, no weeds were included in the harvest (Table 12).

Even casual examination of Table 12 reveals the fact that the yield steadily decreased with thinness of planting. In plots clipped high, the extremes were 299 and 73 grams; in those clipped closely 773 and 233 grams.

TABLE 12. Successive yields from 100 square feet in the several plots cut 6 and 2 inches high respectively; total yields from unclipped plots; and decrease in total forage production resulting from clipping.

Date of clipping	3N		2N		N		½N		¼N	
	6-in.	2-in.	6-in.	2-in.	6-in.	2-in.	6-in.	2-in.	6-in.	2-in.
	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.	gm.
June 22	299	*647*	276	*773*	215	*641*	142	*379*	73	*233*
29	557	*306*	776	*464*	759	*372*	729	*313*	501	*269*
July 8	472	*642*	459	*758*	504	*622*	541	*478*	465	*438*
20	928	*410*	904	*428*	903	*513*	872	*430*	861	*415*
Aug. 1	848	*370*	848	*382*	850	*499*	825	*416*	795	*412*
12	181	*102*	205	*209*	293	*276*	275	*264*	250	*202*
18	2046	*0*[1]	2137	*0*	2368	*0*	2161	*0*	1525	*0*
Total forage produced, gm.	5331	*2477*	5605	*3014*	5892	*2923*	5545	*2280*	4470	*1969*
Forage, unclipped plots	8803		9274		9393		8265		6791	
Per cent decrease from clipping	39	*72*	40	*68*	37	*69*	33	*72*	34	*71*

[1] On August 18, plants in all plots were cut at a height of 2 inches. Those in the closely cut plots had died.

RESULTS FROM PHYTOMETERS

The effects of cutting on water loss and root development in relation to tops were determined by the use of insert phytometers between June 24 and 26. These had been installed, each with 4 plants, at the time of planting in the N plots to be cut 2 inches high and 6 inches high as well as in the unclipped N plots. The total water losses from the plants and 54 square inches of soil surface under the several conditions, respectively, were 482, 995, and 1250 grams. The average dry weight of tops and roots were, in the same order, 0.39 and 0.48 gm.; 1.58 and 0.92 gm.; and 2.73 and 1.9 gm. This was 5 days after the first cutting. These data show that root growth was progressively less with more severe cutting. Moreover, in the closely cut plot, root weight exceeded the weight of the tops. Root volume had been reduced as a result of clipping; the average volumes were 0.48, 0.92, and 1.9 cc. respectively.

SECOND CUTTING

The plants recovered rapidly and made a good growth, especially those clipped high. At the second clipping on June 29, the yields of the taller plants were greatly in excess of those harvested 7 days earlier (Table 12). This was due in part to the closer clipping, which was 6 inches. The greatest yield was no longer from the 3N plot but from the 2N, otherwise the sequence was the same as before. This sequence also held for the closer clippings, the 2N yielding most. In all cases but one, the yields were less than previously, the ¼N alone giving an increased yield.

Results from Phytometers

The effect of clipping on root development was again ascertained from a second lot of phytometers on June 26. These were all from the 2N plots; the plants in two of them had now been clipped twice, 8 and 1 days previously. Dry weight of roots were in the ratio of 100:79:53 as compared to 100:84:61 in the N plots only 4 days earlier (Table 13). Thus one effect of clipping was greatly to retard root growth.

Table 13. Relative root development in the several plots as affected by cutting the tops.

Date	Number of cuttings	Plot	Dry Weight		Volume	
			gm.	Relative	c.c.	Relative
June 26..........	0	N, uncut	1.9	100	16.7	100
	1	N, 6-in.	1.59	84	13.7	82
	1	N, 2-in.	1.16	61	8.2	49
June 30..........	0	2N, uncut	1.04	100	9.3	100
	2	2N, 6-in.	0.82	79	6.9	74
	2	2N, 2-in.	0.55	53	4.6	49
July 21..........	0	N, uncut	3.23	100	17.0	100
	4	N, 6-in.	2.39	74	13.0	77
	4	N, 2-in.	0.68	21	6.0	35
July 21..........	0	½N, uncut	4.55	100	26.0	100
	4	½N, 6-in.	3.13	69	20.5	79
	4	½N, 2-in.	0.94	21	6.5	25

Third Cutting

A third cutting was made on July 8. Although a heavy rain had fallen on June 29 and 30 yet it only temporarily replenished the water in the surface soil. Drought prevailed at least in the thicker planting (Table 6). This undoubtedly reduced the yields.

The highest yield of the 6-inch cutting, 541 grams, was in the ½N plot, and the lowest, 459 grams, in the 2N. There was no regularity of sequence. The highest yield of the 2-inch cuttings was, as before, in the 2N plot. The 3N yielded less, and there was a constant decrease to the thinnest planting. The closely cut plots yielded more than the 6-inch cuttings in all of the thicker plantings, but in the ½N and ¼N they yielded less (Table 12).

Comparative Root Development

The relative root development under the several conditions in the normal plots was determined by direct excavation on July 11 and 12. The depth of penetration in the unclipped plots, those clipped high, and those clipped closely was 68, 58, and 51 inches respectively; the lateral spread was 23, 20, and 20 inches. The number of main roots of the secondary root system de-

creased from 27 to 16 and then to 14. The root tips of the unclipped plants were found distributed more or less uniformly to a depth of nearly 6 feet; on plants clipped high they did not extend much beyond 4 feet; and in the closely clipped group they were largely in the second and third foot. Roots of the closely clipped plants showed a weakened condition and deterioration throughout (Fig. 10 N-c). The average diameter of the roots of the uncut N-plants was 1.24 mm., that of the plants cut closely was 0.78 mm., which was only 63 per cent as great. The average diameter of the stele was 0.662 mm., and 0.320 mm. in the two lots of roots respectively.

Relative Water Content of the Soil

Water content of the soil in all of the plots of the N planting was determined on July 18 (Table 14).

TABLE 14. Water content in per cent in excess of the hygroscopic coefficient at various times in the N plots.

Date	Plot	0 to 4 in.	4 to 12 in.	1 to 2 ft.	2 to 3 ft.	3 to 4 ft.
July 18....	Unclipped..........	14.0	10.9	0.7	4.3	9.2
	Clipped at 6 inches..	15.3	13.4	0.7	9.2	11.4
	Clipped at 2 inches..	16.6	15.0	1.3	10.0	12.4
July 27....	Unclipped..........	9.8	6.3	0.6	3.8	8.2
	Clipped at 6 inches..	7.2	8.9	1.3	6.2	10.6
	Clipped at 2 inches..	6.1	10.3	4.0	8.7	11.7
Aug. 7....	Unclipped..........	—1.3	—0.9	—1.0	2.5	7.9
	Clipped at 6 inches..	—1.8	0.3	0.7	5.8	10.2
	Clipped at 2 inches..	—3.0	1.7	2.5	8.7	12.0

Table 14 shows that there was more water available in the clipped plots than in the unclipped ones. Moreover, water content was higher in the plots where clipping was close and the transpiring surface most reduced.

A rain of 1.2 inches fell on July 7-8 and another of 1.7 inches on July 12. Following these rains water was available at all depths in the N planting, although before the second rain none was available in the surface 4-12 inches of soil (Table 1).

Fourth Cutting

A fourth cutting was made on July 20, after a period of 12 days. Of the plots cut 6 inches high, the 3N gave the highest yield (928 gm.). Yields decreased in the sequence of thinner plantings, the ¼N yielding 861 gm. Among the closely cut plants the N yielded highest, 513 gm., the dry weights decreasing regularly both towards the thinnest and towards the thickest plantings (Table 12).

RESULTS FROM PHYTOMETERS

Immediately following the fourth clipping, on July 21, studies were made on the average dry weight and volume of roots in the three subplots of the N planting. The roots were obtained from large phytometers each of which presented a soil surface of 76 square inches and contained 4 plants. The dry weights, from uncut to closely cut plants, were 3.23, 2.39, and 0.68 grams respectively, and the ratio 100:74:21. Thus the clipped plants had fallen far behind their rate of development under the same conditions after the first clipping when the ratio was 100:84:61 (Table 13). The ratio of the volume of the roots had changed from 100:82:49, on June 26, to 100:77:35, somewhat over three weeks later.

The retarded development of the root systems under the clipping treatment was further shown by roots obtained from similar phytometers from the ½N plots. These data, which are very similar to the preceding, are shown in Table 13. In every case the more closely clipped tops developed the poorest root systems.

DEGREE OF TILLERING

The effect of clipping on development of tillers was determined. The number of tillers on ten of the largest plants selected from each subplot is shown in Table 15.

TABLE 15. Number of tillers on ten largest plants from each of the several plots on July 26.

Plot	Average	Range	Per cent
3N, uncut	3.0	2 to 4	100
3N, 6-in.	16.2	12 to 21	540
3N, 2-in.	20.6	15 to 30	686
2N, uncut	3.5	3 to 4	100
2N, 6-in.	20.2	13 to 29	634
2N, 2-in.	27.1	20 to 33	774
N, uncut	4.5	4 to 5	100
N, 6-in.	25.9	17 to 33	575
N, 2-in.	33.2	22 to 43	737
½N, uncut	6.5	6 to 8	100
½N, 6-in.	48.1	30 to 62	586
½N, 2-in.	52.0	41 to 76	800
¼N, uncut	12.0	8 to 16	100
¼N, 6-in.	54.3	40 to 83	452
¼N, 2-in.	59.4	86 to 88	494

Data in Table 15 show a stimulating effect of clipping upon the production of tillers. The unclipped plants had fewer tillers than the clipped ones, and those clipped closely more than those clipped high. The data also show clearly that tillering increased directly with increased spacing between plants.

RELATIVE NUMBER AND SIZE OF PLANTS

The relative number and size of living plants were also determined in three selected square meters in each of the closely cut, 3N, N, and ¼N plantings. The number of living plants was 195, 76, and 14 in the above sequence, and the dead ones 21, 14, and 1. In the 3N plots there were no plants with more than 40 tillers; 48 per cent had 20 to 40 such off-shoots, and 52 per cent had less than 20. In the N plot the percentages were in the above sequence 6, 39, and 55 but in the ¼N, 60, 20, and 20. Thus while tillering was high in all of the plots it was greatest in the most open stand.

Similar counts in the subplots of the N planting showed that the number of living plants was about the same (80 per sq. m.) in all. But the number of dead plants increased per unit area with closeness of clipping. The degree of tillering also increased in the same sequence. No plant with more than 20 tillers occurred in the unclipped plots; 38 per cent were found among those clipped 6 inches high, and 44 per cent (some with more than 40 tillers) grew in the closely clipped plots.

RELATIVE WATER CONTENT OF SOIL

Nine days later, July 27, another determination of water content was taken in the normal planting (Table 14). Except for the surface layer, the unclipped plants had more thoroughly exhausted the water supply to a depth of 4 feet. The plants clipped high had reduced the water content to a greater degree than the closely clipped ones. The slightly smaller water supply in the 0 to 4 inch layer in the closely clipped plots was due to greater evaporation from the surface soil.

Rate of evaporation from a free water surface was determined by placing 4 soil cans, 7 cm. in diameter and 4.5 cm. deep, each containing 100 cc. of water on the ground in each plot. The average water loss per day during three clear, calm days (July 27-30) was 10, 23, and 40 cc. in the N plots unclipped, clipped high, and clipped closely, respectively.

FIFTH CUTTING

A fifth cutting was made on August 1. Under both heights of cuttings the greatest yields were from the N plot. Yields from the several plots cut 6 inches high were remarkably uniform, only that from the ¼N being somewhat low. All showed a lower yield than at the preceding cutting, probably because the plants were greatly weakened. The yields from the close cutting were far from uniform and higher in the thinner than in the thicker plantings, where the plants withstood cutting best (Table 12).

Eleven days later, on August 7, water content was again determined in the N plots (Table 14). From an examination of Table 14 it is apparent that drought prevailed during the period from July 27 to August 7. Prac-

tically all of the water available for growth was exhausted from the first two feet of soil on August 7. Eleven days earlier, 6 to 8 per cent was available to the 4-inch level and 6 to 10 per cent in the remainder of the surface foot. A study of Table 14 shows that considerable absorption occurred in the third foot (except in the closely clipped plot) but very little in the fourth. Except in the portion of the soil most affected by surface evaporation, the water content, as before, increased directly with the degree of clipping of tops.

SIXTH CUTTING

When the sixth cutting was made on August 12, the water content in the N plot had been reduced to the nonavailable point to a depth of 2 feet (Table 1). The third foot was quite dry and the crop was ripening. In all cases the yields were much lower than for the preceding period (Table 12). The highest yields from both cuttings were found again in the N plots. The yield of the 6-inch cutting was higher than that of the 2-inch one except in the 2N plot where it was only slightly less (Table 12). The yields of the 6-inch cuttings, from the thickest to the thinnest plantings, were only 21, 24, 35, 33, and 31 per cent as great as that of August 1, eleven days earlier. The 2-inch cutting, in the same order, yielded 28, 55, 55, 63, and 49 per cent as much respectively, as before. These decreased yields were due to the weakening or death of the plants, conditions favored by the drought.

MATURE CROP

Dry weather continued, water content was further reduced, and the crop ripened somewhat prematurely. The clipped plants suffered severely and made little growth before drying.

EFFECT OF CUTTING ON ROOT DEVELOPMENT

A study of the relative root development in the N plots was made at the time of harvest, August 17 and 18. The root system in the uncut field reached a depth of 82 inches; in the plot clipped at 6 inches height it penetrated to 67 inches, but in the closely clipped one to only 56. Small differences were found in lateral spread; the spread was about 3 inches less in the clipped plots. Differences in the number of secondary roots were marked, decreasing with severity of cutting from 28 to 19 and then to 16. It was also ascertained that the roots of the plants clipped 6 inches high had died back to about the 4-foot level and those closely clipped to about 3 feet. Great differences in diameters of roots were also found (Fig. 10 N-c).

YIELDS

The closely cut plants had died back after the sixth clipping without further growth. The large yields of the plots cut 6 inches high were due to the

last cutting being made at 2 inches height, in order to obtain the total production of forage.

The total yield from the unclipped plots was greatest from the N rate of planting. Considering this as 100 per cent, the other yields were, 2N, 98 per cent; 3N, 93; ½N, 88; and ¼N, 72 per cent.

The total forage produced by the plants cut at 6 inches height was, in order of amounts, N, 2N, ½N, 3N, and ¼N. Comparing the total yields of the 6-inch cuttings with those of the unclipped plots of similar densities the losses from thickest to thinnest plantings were 39, 40, 37, 33, and 34 per cent respectively.

The most forage produced from the 2-inch cuttings was from the 2N plot, with decreasing yields in the following order: N, 3N, ½N, and ¼N. The total decrease in yield was greater from the 2-inch cuttings than from the plants cut at 6 inches height. Compared to the yields from the 3N to ¼N unclipped plots, the decreases were 72, 68, 69, 72, and 71 per cent. Thus while the decrease in total yield averaged about 37 per cent for the plants clipped high, the average where the plants were clipped closely was 70 per cent.

Discussion

A study of the graphs showing the yields produced at each cutting reveals several pertinent facts (Fig. 16). The plants cut at 2-inches height yielded most in the 2N plots during the first three clippings, but in the N ones during the last three. Thus an average increase in yield of 22 per cent was gained by doubling the rate of planting, but after the third clipping there was none. Maximum yields from the plots cut 6 inches high were less consistent, shifting from the 3N through the 2N to the ½N and then back to the 3N. After the third cutting, however, the yields from the several plots were fairly uniform, except the last, the two thinnest plantings consistently yielding somewhat less.

After the plants had once been clipped, the new growth yielded more where they had been clipped high than where they had been clipped closely. An exception occurred in the N and more thickly planted plots at the third cutting, but the causes were not evident. General differences in yields at each cutting varied because of unequal periods for growth between cuttings, environmental conditions, and degree of exhaustion of the plants. The greater yields from the higher cuttings are to be explained upon the basis of the greater photosynthetic area retained after cutting. At the time of the first cutting the shoots were two feet high and the root systems were growing vigorously and probably had little accumulated food. There were 13 main roots, the longest being about 3 feet.

Repeated cutting back of the shoot stimulated tillering. Once formed, the tillers were least injured by successive cuttings and developed bushy

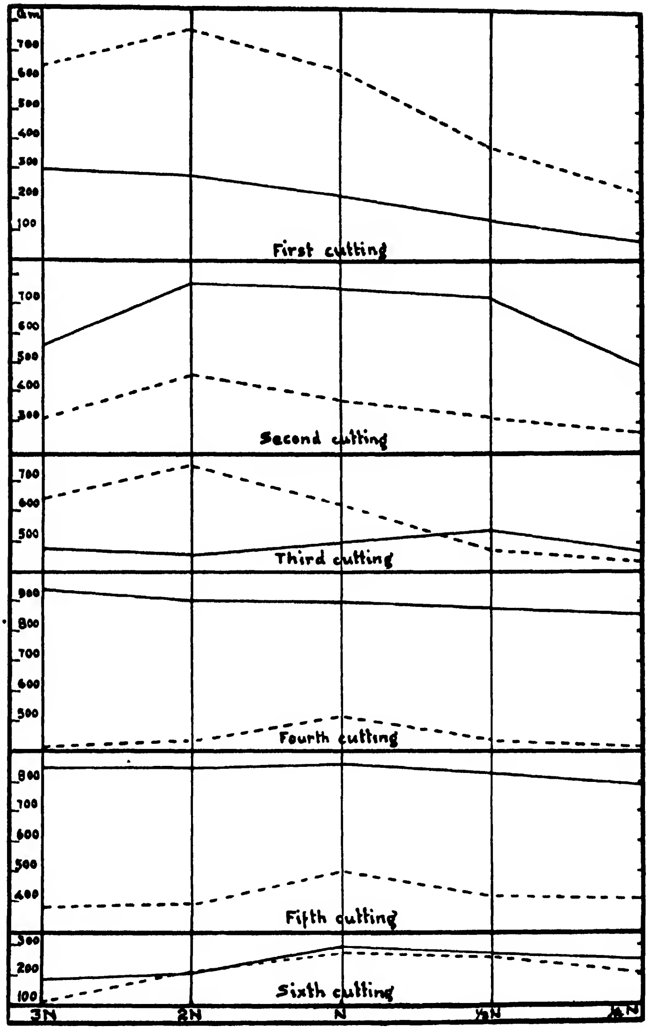

FIG. 16. Yields from 100 square feet of each plot at the several cuttings. Solid lines represent cuttings at 6 inches height, except the first which was 9 inches; broken lines, cuttings at 2 inches height.

plants. After two or three clippings the stem of the mother plant died. After the fourth cutting, tillering was greatest in the closely cut and least in the uncut plots. The greater degree of tillering in the closely clipped plots was due to the development of latent buds at the basal nodes, many of which could not have grown had the supplies of food materials and foods been used in the production of a large parent stem. The repeated clippings also harmed the growing tillers until finally the plants died of starvation and drought. Drying of the surface soil was accentuated by the removal of weeds. But

under normal conditions they would have competed for water and finally overtopped the Sudan grass. Harrison (1931), and Biswell and Weaver (1933) state that the deleterious effect of frequent cutting may, however, be offset partially by cutting the plants at a greater height above the ground.

Sudan grass is a strong competitor of weeds. This is due to its rapid growth and great height. The leaves are quite tolerant of shade, remaining green at the 12-inch level in the 3N plot after rough pigweed, crab grass, and cultivated sunflowers had succumbed. A decided advantage of moderate grazing is that of weed control.

The extent of root development correlated with the extent of tops. The uncut plants increased their dry weight of roots 70 per cent from June 26 to July 21, a period of 26 days. The roots of plants cut 6 inches high four days before June 26, and thrice more before July 21, showed an increase of 50 per cent during this 26-day period. But where the tops were cut 2 inches high at these same periods, the dry weight of the root decreased 41 per cent (Table 13). In the last case, although a few new roots were added in the surface soil, the established roots died back from their tips for a considerable distance in the deeper soil. Sturkie (1930) found that any cutting treatment of *Sorghum halepensis* L. reduces the rootstock development, and the more frequently the cuttings were made the greater was the reduction. This was due to depletion of food reserves in the roots. Aldous (1930) has shown that "cutting frequently or cutting at maturity depletes the reserves in the roots of herbaceous plants."

The effect of clipping of the tops of Sudan grass not only affected the amount of dry weight of the roots, but also the extent of root penetration, size, and number of roots of the secondary root system. This is in accord with the findings of Robertson (1933) who states that removal of tops invariably retarded root penetration and sometimes stopped it completely. Biswell and Weaver (1933) also found that the roots of the clipped grasses yielded only 2.6 to 20.6 per cent as much as unclipped ones. They were also smaller in diameter than were those of the controls. The diameters of the roots of frequently cut *Poa pratensis* L. and *Panicum virgatum* L. were only 76 and 64 per cent respectively as great as those of the controls.

There was but slight difference in the total spread of the roots of the uncut and cut plants. This was due to the fact that when the first cutting was made on June 22, the lateral spread of the roots had already reached a maximum, the general area for root penetration being nearly blocked out (cf. Weaver, 1926). The number of mature roots per plant varied greatly, from 28 in the control to 19 in those clipped high and to only 16 in those clipped closely.

The leaf area of the tops was somewhat in proportion to the available water content of the soil as well as to the available light. Results of repeated

determinations of the water content in the uncut plots showed that where drought was greatest, in the soil layer in which the roots were distributed, the leaf area was least.

The effects of competition were accentuated by the dry summer and the relationships between factors and plant development were probably more marked than they would have been had the season been one of abundant rainfall.

SUMMARY

Sudan grass was grown on level, deep, fertile, sandy loam soil at Lincoln, Nebraska, during the dry, hot summer of 1933. Its life history was determined under the normal rate of planting, the effects of competition under different rates of planting, and the behavior of plants under different heights of cutting.

Planted on May 22 at the rate of 22 pounds per acre, development was so rapid that during the 20 days of the seedling stage the roots grew at an average rate of 0.75 in. per day and the tops developed 7 leaves and reached a height of 13 in. The length of the single primary root (13 in.) was exceeded by the first roots of an elaborate secondary root system, and the general area to be occupied by the roots was blocked out.

During the following 20 days of tillering, the roots grew an inch per day and reached a depth of 4.1 ft. In extent, they still exceeded the tops, which were 3.8 ft. tall and had developed 4 tillers, the first appearing 17 days after planting.

A height of 7.5 ft. and a root depth of 6.8 ft. were attained during the following 47 days of flowering and maturation. Rate of root growth decreased to 0.8 in. per day, the mature root system, consisting of 28 main roots, occupying a volume of soil 2 ft. wide and 6.8 ft. deep. Only one of the 5 tillers bore a panicle; that of the parent stalk was 12 in. long and produced 6 grams of grain.

Increase in dry weight (to 14.1 grams when in flower) always exceeded the increase in area of green leaves (maximum, 207 sq. in.), since, owing to drought, most of the lower leaves died.

This grass is adapted to drought by its prompt germination when water is available, by its rapid root penetration into the deeper soil, and by its ability to become dormant during drought and recover thereafter.

Sudan grass is a heavy consumer of water, due to its rapid development and great leaf area resulting from abundant tillering. Although 9 in. of rain fell during its 87 days of growth, the moist soil at the time of planting had lost practically all of its available water at harvest.

Competition, in plots 25 by 40 feet each, was measured under normal rate of sowing (N), 2N, 3N, ½N, and ¼N rates. Differences in height

were not marked until rapid stem elongation occurred about July 1. The less crowded the plants the more able were they to manufacture materials for growth of stems, hence the plants became increasingly taller from the 3N to the ¼N plots. The same relationships attained, throughout the entire period of development, as regards length, width, and area of leaves, diameter and area of stems, number of tillers, size of panicles, and dry weight of tops, as well as number and depth of roots.

Length of mature leaves varied from 18 in. (3N) to 23.7 in. (¼N), and width of leaves from 22 mm. to 38 mm. The maximum area of green leaves (Aug. 2) was 44.3 sq. in. per plant in the 3N plot and 692.3 sq. in. in the ¼N. The average area of green leaves per square meter, on July 1, was 104 sq. ft. and 47.7 sq. ft. The thinnest planting had nearly 45 per cent as great an area of leaves as the thickest, but only 5.2 per cent as many plants.

Leaves in the thicker plantings were much thinner, the veins were more closely spaced, and the cells much smaller than in the thinner plantings. Osmotic pressure of cell sap of leaves increased progressively from 10.6 A. (3N) to 14.2 A. (¼N).

Diameter of stems ranged from 5.9 mm. (3N) to 10.8 mm. (¼N). The range in average height was from 6.2 feet to 8 ft., but the range in area of stems was far greater, from 21.3 sq. in. in the 3N to 250 sq. in. in the ¼N.

The maximum number of tillers varied from 3 in the 3N to 4 in the N and 10 in the ¼N.

The average length of panicles varied from 25.3 cm. (3N) to 37.5 (¼N); the width from 14.9 to 31.5 cm., and dry weight of grain from 3.6 to 13.9 grams.

The reduction in growth of roots in the thicker plantings was nearly in proportion to the reduction of tops during the first five weeks, but later, as a response to the drying soil, roots showed a greater development than the tops. Depth of penetration ranged from 74 in. (3N) to 90 in. (¼N); spread of roots from 9.6 to 32 in.; and number of main roots from 17 to 44. Roots were of smaller diameter in the thicker plantings, ranging from an average width of 0.884 mm. (3N) to 1.77 mm. (¼N).

Water losses from large, insert phytometers, were greatest both per unit area and per plant with increased thinness of planting. Losses per unit area of green leaves were greatest in the thinner stands during the seedling stage but later they became greater in the thicker plantings.

Repeated determinations of available water content of soil showed uniformly that competition for this factor was most severe in the thickest planting and progressively less so to the thinnest. Water was a chief limiting factor for growth; the degree of plant development was in direct relation to the amount of available water.

Light ranged from 23 to 60 per cent from thickest to thinnest plantings

when the plants were about 46 inches tall, but from 11 to 32 per cent when they had attained full stature. Relative humidity decreased with thinness of planting, evaporation also increased.

The yields of cured hay per acre in the order of thickness of planting were (¼N) 3.25, 3.96, 4.50, 4.44, and 4.22 tons respectively; considering the N yield 100 per cent, they were 72, 88, 100, 99, and 94 per cent.

Plots 20 by 25 feet in each thickness of planting were cut 6 times at a height of 6 inches, and another lot (15 x 25 feet) at 2 inches. Maximum partial yields from plots cut 2 inches high were from the 2N or N plantings; those from the 6-inch cuttings varied widely. After the plants had been clipped once, subsequent yields were greatest from those that had been clipped high.

Repeated cuttings of the tops caused the death of the parent stalk and stimulated tillering, plants cut closely tillering most. Due to its rapid growth and great height, Sudan grass is a strong competitor of weeds, but its repeated cutting favors their development.

Extent of root development correlated with extent of tops. Increase in dry weight of roots was 70, 50, and —41 per cent in the N uncut plants, those cut high, and those cut closely, respectively, during a period of four cuttings.

The uncut plants had 28 main roots; those cut at 6 inches height, 19, and those cut at 2 inches height, 16. The last, which were much smaller in diameter, had died back from the tips. These closely cut plants finally died of starvation and drought. Use of water, especially below 2 ft., was least in the closely clipped plots, and greatest in the unclipped ones.

The total yields decreased as a result of clipping 6 inches high, from 3N to ¼N, 39, 40, 37, 33, and 34 per cent. Decreases where the clipping was at 2 inches height were 72, 68, 69, 72, and 71 per cent.

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VIABILITY AND GERMINATION OF SEEDS AND EARLY LIFE HISTORY OF PRAIRIE PLANTS

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CONTENTS

VIABILITY AND GERMINATION OF SEEDS AND EARLY LIFE HISTORY OF PRAIRIE PLANTS*

INTRODUCTION

The viability and germination of the seeds and the early development of the seedlings of cultivated crops have received much attention (Duvel, 1904; Weaver, 1926; Weaver and Bruner, 1927; Edwards, 1932). Seed testing has become a part of the routine work of federal and state agricultural departments (Harrington, 1916; U. S. Dept. Agr., 1927). Experiments have been made also on the development of weed seeds (Fawcett, 1908; Oswald, 1908). In connection with problems of reforestation and afforestation, the seeds of trees have been the objects of much research (Hofmann, 1917; Korstian, 1927). Rather recently in range investigations, a few similar studies have been made on the native species of the drier portions of the grassland (Sarvis, 1923; Wilson, 1931).

Practically no work of this nature has been done in the region of tall-grass prairie, centering in Kansas and Nebraska. Native grasslands furnish a very different problem from that of cultivated crops or weeds, since the conditions for germination and establishment are quite different. This research was done at Lincoln, Nebraska. The object was to determine the viability and germination of seeds of prairie plants and the conditions for establishment in the prairie.

The problem was suggested by Dr. J. E. Weaver. The writer wishes to express deep appreciation of the privilege of working under the direction of one who is so thoroughly acquainted with the ecology and physiology of the vegetation of the prairie.

Seeds of the common species were collected each fall during 4 years, from 1928 to 1931. Their viability and germination were tested by planting in soil, usually in the greenhouse. Studies were made of seedlings found in the prairie and of seedlings germinated in sod brought into the greenhouse. Early development was observed from seeds sowed in the greenhouse and in the prairie.

ENVIRONMENT

So closely are the environmental factors of water content of soil, temperature, evaporation, and light related to viability, germination and establishment, that at least brief consideration must be given them. Weaver and Himmel (1931) have recently summarized the factors from measurements made in the field over a period of 12 years.

"Water content and humidity are the master factors of the environment of the prairie. . . . Water content in the surface 6 inches of upland soil varied

* Contributions from the Department of Botany, University of Nebraska, No. 94.

widely and rapidly, often 10 per cent or more during a single week." It approached exhaustion, measured by the hygroscopic coefficient, from one to four times during the growing season. In the surface 3 inches the fluctuations were much more extreme; here the available water was often entirely exhausted. At 6 to 12 inches it was reduced to 2 to 3 per cent once or twice during the season. Below the first foot, the water content was not critical, though the available supply sometimes fell to 5 per cent.

"A close positive correlation was found between precipitation and water content, especially in the surface 6 inches. . . . The mean annual precipitation is 28 inches, of which nearly 80 per cent falls during the growing season." Fourteen inches fell during May, June, and July. For the months important in germination and establishment, the average rainfall of April is under 3 inches, that of May and of June is a little over four. "The rainfall of May and June is usually well distributed but that of July and August is less so. . . . A rainfall of less than 0.20 inch is probably entirely intercepted by the vegetation and the dry surface half-inch of soil", where its effect is extremely temporary. "Drought periods of 15 days or more when the rainfall on consecutive days did not exceed .20 inch occurred every year. . . . That they are rather regularly distributed throughout the growing season is shown by the fact that 6 occurred in April, 9 in May, 5 in June, 9 in July, 7 in August, and 8 in September. . . . The light, scattered showers during such times are of little significance in increasing the water content." The lowering of temperature and increasing of humidity, which are the chief effects of brief showers, are rapidly counteracted by subsequent bright sunshine and wind. Not only is the development of seedlings influenced by such periods of drought but also the process of pollination. In the extreme, long-continued drought of 1930, upland species generally ceased to bloom. The germination of the seeds of the harvest of that year was lower, for many species, than from any of the other years of the study.

"Nebraska has much sunshine; 175 to 185 clear days occur and only 81 to 86 completely cloudy ones. During March, April, and May there is approximately 60 per cent sunshine but June, July, and August have 72 per cent or more."

"Temperatures of air and soil during the long growing season are well within the ranges critical for plants of the prairie and are probably of secondary importance." The average day temperatures of the air were usually between 75° and 85°F. The night temperatures were ten degrees or more lower. The average soil temperature at a depth of three inches was 56° in April, 68° in May, 78° in June, 84° in July, 81° in August and 73° in September. Daily variations of 15° to 18°F. were shown at this depth, but only 1° to 3° at 12 inches. Seeds were thus subjected to considerable fluctuation, a generally stimulating influence for germination (Fivaz, 1931).

"Humidity, through its direct control of transpiration and evaporation from the surface of the soil, frequently determines whether a plant can or can not grow in a given habitat. It must be considered in all problems concerning the distribution of vegetation." During wet years the average day humidity was 50 to 60 per cent. During dry years it was 40 to 50 per cent, falling as low as 15 to 30 sometimes in the late afternoon.

Wind movement, important in the prairie because of the lowering of humidity, is often high. The average hourly velocity is 10.7 miles. "It is fairly constant throughout the year. It reaches a maximum of 13.2 miles per hour in April and decreases gradually to a minimum of 8.7 miles in August." It has frequently less than half these velocities at the six-inch level among the grasses. "Even a movement of 4 to 5 miles per hour greatly increases transpiration. . . . Data show conclusively that the wind is an important environmental factor." The chief effect on establishment is probably through the withdrawal of water from mature vegetation. The small shoots of the seedlings, in the relatively humid atmosphere near the ground, are protected from increases in transpiration. They must, however, have abundant water to continue growth. Indirectly the wind is a powerful influence in depleting the water supply.

"Evaporation varied greatly from year to year. At a height of 2 to 5 inches above the surface of the ground it was usually between 20 and 30 cc. per day, as computed from weekly losses. During periods of drought it sometimes reached 40 to 55 cc. High evaporation was correlated with low humidity and both of these with low water content of soil."

The Prairie Sod

The prairie is a closed formation. The mass of vegetation is limited by the available water. To within half an inch of the surface, the upper 3 to 6 inches of soil are occupied by roots and rhizomes, and occasionally by bulbs, corms, tubers, and their outgrowths. The dense network of roots extends much deeper. Everywhere the soil is compacted and so thoroughly threaded with plant parts as to form a sod. So well developed is the network of absorbing rootlets that, between absorption and direct evaporation from the surface of the ground, water content of the shallower soil is often reduced below the point available for growth.

More than 95 per cent of the species are perennial. Many of them have a life-span of 10 to 20 years. In competition with these, seedlings find establishment difficult. The large percentage of sunshine, the irregularity of precipitation and the frequent occurrence of high winds after showers are physical factors which combine to keep the surface moisture low. The wetting of the soil around the seed may be too transitory for germination to be effected. Either the seed may fail to swell or, after the embryo has

FIG. 1. Typical upland prairie in late September, after mowing and stacking of hay. (Photo by Weaver).

assumed active growth, it may be destroyed by sudden desiccation. Very frequently the falling seeds are caught and held in the crowns or among the dead stems or leaves of old plants (Fig. 1). If enough water is obtained for germination, the rootlet is in danger of becoming dried beyond recovery before it can elongate into the soil.

The need for water is of first importance. The adjustment to this is rapid penetration. A good root is formed before the shoot appears above ground. A deep absorbing system is produced before much leaf surface is developed (Fig. 2). While these earliest stages of development are progressing in the spring, the established vegetation is adding rapidly to its annual growth of tops. This results in increased competition for water. At the same time there is introduced the factor of reduced light intensity. Practically all prairies are mowed annually. The sod, however, is unbroken. The general effect of removing the foliage cover may not be greatly unlike that produced, under more primitive conditions and more scattered populations, by frequent prairie fires. Shoots start to grow sooner and more vigorously when exposed to the light and warmth of the sun's rays than when they must elongate through a tangle of dead plant parts. According to Weaver and Fitzpatrick (1934) the surface of the soil actually occupied by shoots of grasses and forbs varies from 6.5 to 37 per cent. Sod-forming and bunch-

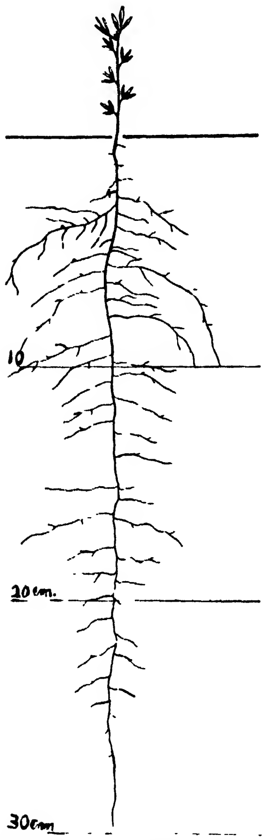


FIG. 2. *Petalostemon candidus* about 6 weeks old, showing rapid penetration of taproot to 30 cm.

forming grasses constitute the bulk of the vegetation. The forbs add an important but variable amount. With an average basal cover of about 15 per cent, the vegetation may have a foliage cover of 100 per cent; that is, the soil may be entirely concealed by the plants when viewed from above. By June the shade under the long established plants has become so dense that seedlings are unable to make adequate carbohydrates for vigorous growth. Before midsummer the light is often reduced to 30 per cent at a height of 12 inches and to 5 per cent at the ground level. The retardation of development usually results in starvation and death (Clements, Weaver, and Hanson, 1929).

VIABILITY OF SEEDS

The absolute viability of seeds can be tested only by very delicate laboratory methods. These include the detection of an electric current, when an induction shock is sent through a living seed which is connected with a

galvanometer, and the observation of an increase in the output of carbon dioxide, when living seeds are electrically stimulated (Tashiro, 1917).

The practical test for viability is germination. A seed must have sufficient vitality to develop a seedling and to maintain it until it is able to support itself. Otherwise there is little significance in the mere demonstration that the embryo possesses enough living protoplasm to make a response to a violent stimulus of an abnormal nature.

General Methods of Testing

The accepted method of seed testing is to expose known numbers of seeds to conditions favorable to germination, usually between layers of moist, absorbent paper or in sand or soil. The numbers of seeds which germinate in a given time are calculated on a percentage basis. The standard of germination is arbitrarily fixed. Most often it is regarded as the projection of both root and plumule beyond the seed coat or as the appearance of the first leaf above ground. Failing to meet such a test, seeds are considered non-viable (Zinn, 1920).

Discussion

For the seeds of ordinary crop plants tested on a commercial scale; such a standard, supplemented by a rigid time limit, has proved satisfactory. One important factor, however, is disregarded. This is dormancy. It may be either primary, due to the condition of the newly formed embryo or seed coat, or secondary, from a relapse into a state which inhibits the resumption of growth.

Cultivation, owing to practical considerations of seeding and harvesting, has resulted in varieties of field and vegetable crops which show much uniformity of behavior. The seeds of most domesticated crops possess very brief latent periods, easily broken under conditions suitable for germination. Native seeds and those of a large number of woody plants classed as "ornamentals" are characterized by long periods of dormancy, frequently recurrent and difficult or impossible to break.

Fawcett (1908) tested germination of weed seeds in Iowa. From plantings at intervals of one month, he concluded that two periods of activity existed, spring and fall, with deep dormancy during the other months.

Howard (1915), working in Missouri for the most part with species other than grasses, found that the larger number of native seeds, planted out-of-doors as soon as they ripened in the summer or fall, did not germinate before the following spring.

Schmidt (1929) observed periodical or seasonal variations in germinative energy. In *Pinus sylvestris*, for example, they were very distinct, with maxima in March-April and minima in late autumn and January.

Darlington (1931), continuing Beal's fifty-year experiment in Michigan,

had occasion to change the time for testing germination from fall to spring. The tests, made at five-year intervals, had been showing successive decreases both in species possessing viable seeds and in numbers of seedlings which germinated. The spring planting yielded a higher record of viability than had been obtained five years earlier.

Wilson (1931), in New Mexico, tested the germination of native grasses for possibilities for range planting. His extensive tables give dates of planting and percentages of germination which suggest the same characteristic.

Death is slower to overtake the seeds of most species when they are stored artificially than when lying in the ground. In addition to the hazards of being consumed by animals or injured by fungi or bacteria, they are exposed to alternate wetting and drying and freezing and thawing. Doubtless many seeds perish because they have begun germination at an unfavorable time. After the seed coats have swollen and the protoplasm of the embryo has been altered to an unstable, more active condition, a sharp decrease in moisture or temperature may desiccate the tissues so rapidly that their essential structure is destroyed.

TESTS OF VIABILITY

Successive plantings of seeds of 10 common prairie species were made at intervals of about 2 months for a year following the collection of seeds in the fall of 1930. Successive plantings of the same species were made at intervals of about one month, following the harvest of 1931, for a period of 8 months. Seven grasses and 3 freely germinating forbs were employed. The list comprised big bluestem (*Andropogon furcatus* Muhl.[1]), little bluestem (*A. scoparius* Michx.), blue grama (*Bouteloua gracilis* (H. B. K.) Lag.), nodding wild rye (*Elymus canadensis* L.), tall panic grass (*Panicum virgatum* L.), Indian grass (*Sorghastrum nutans* (L.) Nash), a dropseed (*Sporobolus asper* (Michx.) Kunth), prairie false boneset (*Kuhnia glutinosa*, Ell. (*K. suaveolens* Fresen.)), a blazing star (*Liatris punctata* Hook.), and common evening primrose (*Oenothera biennis* L.). The hairy grama (*Bouteloua hirsuta* Lag.) and tall marsh grass (*Spartina michauxiana* Hitch.) were included, each for one year.

The plantings were in soil, on benches in the greenhouse. The early plantings were from unfrozen seed. As the seeds were stored at out-of-doors temperatures, a change was made, with the advance of winter, to the use of frozen seeds. Each planting was allowed a period of two months before the count of seedlings was discontinued. Lots of 100 seeds, single or in duplicate, were planted.

The longevity of the seeds of 7 species of grasses and 4 of forbs from one harvest was also tested during four consecutive years. The seeds were kept in dry storage at room temperatures until they were planted. Two

[1] Authority for the name of the species is given only the first time the name is used.

hundred seeds of each species, in duplicate lots of 100 each, were sowed annually in March from 2.5 to 5.5 years after the harvest. The grasses included *Andropogon furcatus, A. scoparius, Elymus canadensis, Koeleria cristata* (L.) Pers., *Sorghastrum nutans, Sporobolus asper*, and *Stipa spartea* Trin. *Oenothera biennis, Kuhnia glutinosa, Liatris punctata*, and *L. scariosa* (L.) Willd. (*L. aspera* (Michx.) Greene) composed the list of forbs.

RESULTS

Power of germination increased gradually from very low or none at harvest time to a maximum in mid-spring. This was followed by a distinct lowering during summer and a marked rise in early fall. If the spring planting was exposed to unfavorable conditions, the germination in early autumn (from seeds of the previous fall) usually was maximum for the year (Tables 1, 2).

Seasonal variability in the time of ripening of seeds was illustrated by a comparison of the earlier plantings of the two years. After the dry, hot summer of 1930, the grasses usually germinated to some extent in October and showed a marked increase in seedling production two months later. The following year there was practically no germination immediately after harvest and very little, in most instances, for several months.

Oenothera biennis in the first year of the study displayed the frequently noted phenomenon of germination at harvest time, followed by complete absence of seedling development for a relatively long period (Crocker, 1916).

Monthly fluctuations of considerable magnitude were the rule with all species. Lack of uniformity of external conditions was undoubtedly responsible to some extent. Such variability is much greater for seeds planted in soil in a general greenhouse than in a thermostatically controlled germinator. The fluctuations, however, are far less extreme than they would be under natural conditions. They should suppress merely the weakest seedlings. These, if developed under uniformly optimum moisture and temperature and without the obstruction of soil to be penetrated, give a false impression of the possibilities of natural germination.

The annual tests of 7 grasses from 2.5 to 5.5 years after they were placed in dry storage at room temperatures displayed, at the end of that period, increased germinative power for 2 species and very marked reduction for 5 species. *Elymus canadensis* decreased in germination from over 95 per cent in its third year to one per cent in its fifth year. Two species of Andropogon and *Stipa spartea* were reduced in their sixth year to about one-tenth of the germination which they gave in their third year. For *Andropogon furcatus* and *A. scoparius* the loss in germinating power developed suddenly, between the fifth and sixth years. *Koeleria cristata* diminished from 21 per cent in the third year to 7 per cent in the sixth. The germination obtained in the pre-

TABLE 1. Percentage germination of seeds of 1930 planted at intervals from October 1930 to September 1931

Species	October 9	December 10	January 10	February 10	April 12*	May 8	June 20	July 18	August 29	September 16
Andropogon furcatus	1.0	....	4.5	3.0	6.0†	....	6.0†	....	3.5	....
Andropogon scoparius	3.0	8.0†	....	1.5	1.0	....	2.5	5.0	8.0†	....
Bouteloua gracilis	5.0	31.0†	...	25.5	18.0	....	24.0	....	15.0	....
Bouteloua hirsuta	0.0	5.0	....	6.0	9.0	....	3.5	....	21.5†	....
Elymus canadensis	37.0	....	....	38.0	25.5	....	31.0	....	45.5†	....
Sorghastrum nutans	4.0	6.0†	....	3.5	0.5	....	0.5	....	4.5	....
Sporobolus asper	0.0	60.0	....	40.5	....	15.0	....	24.0	....	65.0†
Kuhnia glutinosa	0.0	45.5	42.0	....	....	57.0†	....	39.0	....	46.0
Liatris punctata	3.0	40.0	47.0†	....	....	41.0	....	15.0	....	21.0
Oenothera biennis	9.0	0.0	....	3.5	....	55.0†	....	28.5	....	....

TABLE 2. Percentage germination of seeds of 1931 planted at intervals of one month from October 1931 to June 1932

Species	October 6	November 10	December 11	January 11	February 15	March 18	April 23	June 3
Andropogon furcatus	0.0	0.0	7.0	11.0	9.0	5.0	20.0†	3.0
Andropogon scoparius	0.5	0.0	0.0	1.0	3.0	0.0	5.0†	2.0
Bouteloua gracilis	0.0	3.0	1.0	5.0	10.5†	10.0†	10.0†	0.0
Elymus canadensis	....	5.0	....	76.0	78.0	....	87.0†	69.0
Panicum virgatum	0.5	0.0	0.0	0.0	0.0	0.0	14.0†	1.0
Sorghastrum nutans	0.0	0.0	0.0	0.0	1.0	1.0	5.0†	1.0
Spartina michauxiana	0.0	0.0	0.0	1.0	3.0	....	6.0	7.0†
Sporobolus asper	1.0	0.0	0.0	1.0	15.5	32.0	91.0†	18.0
Kuhnia glutinosa	6.0	36.0	14.0	49.0	38.0	55.0†	51.0	17.0
Liatris punctata	....	7.0	19.0	54.0	67.0	83.0†	70.0	30.0
Oenothera biennis	0.0	0.0	0.0	0.0	1.5	2.0	13.0	17.0†

*The week following planting in April, 1930 was extremely hot. Low germination of most species was due in part, probably, to drying of the sprouting seeds in the soil.
†Maximum germination.

ceding year was very much lower, emphasizing again the inadvisability of depending on a single test as a basis for conclusions on wild seeds. *Sorghastrum nutans* and *Sporobolus asper* gave their maximum germination in the sixth year. *Sorghastrum nutans* alternated between approximately 15 and 25 per cent throughout the entire experiment. *Sporobolus asper* showed a steady increase from 16 per cent (a low figure for the species) in the third year to 67 per cent in the sixth year (Table 3).

The three composites which were all of one tribe, *Kuhnia glutinosa, Liatris punctata,* and *L. scariosa,* gave no germination in their sixth year.

Large decreases were observed between the fourth and fifth years. *Oenothera biennis* developed a reduction of 50 per cent between the third and sixth years.

The decrease in germinative power was usually accompanied by marked lengthening of the time interval between planting and the appearance of the largest proportion of the seedlings. As the seeds near their limit of life, even in the presence of abundant moisture and suitable temperatures, the chemical reactions which must take place if the protoplasm is to resume an active state, occur slowly or not at all. The generalization frequently made, that species of high and prompt germination are short-lived, was supported by the record of *Kuhnia glutinosa* and contradicted by that of *Sporobolus asper*.

Conclusions

Germination is the practical test of viability of seeds. It fluctuates from month to month for any single lot of seeds of prairie plants. For many species these monthly variations may be large enough to obscure the real viability. A general tendency to yield maximum germination in the spring was seen for native seeds of the prairie region of the central United States. Several species showed a second period of high germinative capacity in early fall, after nearly a year of storage. Immediately after harvest, germination usually was very low. When germination is made the test of viability, it should be tried at the time of year most favorable to the development of the seeds.

Seeds of several common species, kept in dry storage at room temperatures, lost their germinative power within six years. Under the hazards of storage in the surface soil in a prairie climate, their length of life would often be shorter. With the exception of sporadic individuals with unusually hard coats and high vitality, the period of viability in native sod is probably less than five years.

GERMINATION

The germination of seeds of prairie plants was studied in several ways. The most extensive work was in determining the percentage germination of seeds collected in the field when ripe and planted in soil in the greenhouse. Harvests of four consecutive years were tested for 13 grasses and 18 forbs,[2] and for three consecutive years for 2 other grasses and 9 other forbs. In addition several herbs were tested for one or two seasons.

Germination of seeds which had fallen naturally in the prairie was recorded both by list quadrats of seedlings found in the spring and fall during the period of study and also by bringing sod into the greenhouse late in the fall, after most seeds had fallen, and listing the seedlings which developed. These studies of germination in prairie sod were pursued during four consecutive years.

[2] *Amorpha canescens*, a half-shrub under natural conditions, behaves as an herb under mowing. It has been included because of its great abundance and importance.

TABLE 3. Changes in percentage and time of germination of seeds of 1926 planted at intervals of one year*

Species	Germination	1929	1930	1931	1932
Andropogon furcatus	Percentage	13.5	18.5	11.0	1.5
	Time	7	9	12	12–19
Andropogon scoparius	Percentage	8.5	6.0	6.5	1.0
	Time	11	11	31	14
Elymus canadensis	Percentage	96.5	....	1.0	1.0
	Time	10	....	80	33–40
Koeleria cristata	Percentage	21.0	....	0.5	6.6
	Time	10	....	31	12
Sorghastrum nutans	Percentage	14.0	23.5	15.5	26.0
	Time	10	14	12	14
Sporobolus asper	Percentage	15.5	19.5	48.5	67.0
	Time	18	11	14	7
Stipa spartea	Percentage	52.0	....	26.0	5.0
	Time	11	....	13	14
Kuhnia glutinosa	Percentage	26.5	26.5	1.5	0.0
	Time	4	7	25	....
Liatris punctata	Percentage	74.0	52.5	0.0	0.0
	Time	10	8	....	....
Liatris scariosa	Percentage	74.0	81.0	20.0	0.0
	Time	10	11	21	....
Oenothera biennis	Percentage	68.5	....	....	34.0
	Time	8	....	....	19

*Seeds were planted in March. The time of germination is recorded as the number of days when the largest proportion of seedlings appeared.

Problems treated in connection with the percentage germinations of planted seeds include the determination of optimum water content of soil; the effect of freezing, both in dry storage and in moist soil; and the length of the period of dormancy after planting.

TESTS OF GERMINATION

Seeds were collected during their natural period of dispersal in the field and tested for germination during the following winter and spring.

METHODS

The seeds were spread out in the air for a few weeks to promote drying. A small quantity of the seeds of each species was stored in the house and kept at room temperatures until planting. The remainder were stored out-of-doors in cloth sacks protected from precipitation, so that they were subjected to dry freezing from a few weeks to a few months before being planted. Winter temperatures during the 4 years of the study averaged 32°F. for December, 21° for January, 32° for February, and 38° for March. During each of these months fluctuations between average maximum and average minimum temperatures amounted to 15 to 20 degrees. During each winter except the unusually warm season of 1930-1931 temperatures below zero were recorded in 2 consecutive months.

Four hundred seeds of each species were planted. Two hundred of these were from frozen storage, 200 from unfrozen. Both lots were sowed in du-

plicates of 100 each. Occasionally it was necessary to use smaller numbers. Seeds which were conspicuously undersize or poorly filled were avoided when possible.

Examination of the seeds of *Agropyron smithii* Rydb., a species which had given very poor germination, was made, in the fourth year, for the presence of embryos. The seeds were spread in a single layer on a glass plate, illuminated from below by an electric light. By the use of a hand lens it was seen that many of the glumes were empty. These were discarded. This method of improving the chances of germination was very efficacious. It is prevented by the structure of many seeds and is too slow to be practical. It indicates a common cause of low germination.

The seeds were planted in soil on benches in the greenhouse. The soil employed was derived from prairie sod. The appearance of the seedling above ground was the test of germination. After identification the seedling, together with the seed when possible, was removed with little disturbance of the soil. Otherwise damping-off was likely to cause errors in the record.

The first year the seeds were left in the soil for a period of 5 to 6 months. Since most of the germinations occurred during the first 2 months, the length of the test was reduced, after the first year, to 3 months. In the first 3 years the plantings were made in January and February following the harvest. The fourth year all of the sowing was done during the last two weeks of February. Many of the species were also planted at other times during the year. In summer, tests were made in the garden instead of the greenhouse. When more than one test of the previously frozen seeds of a species was made during a year, the one yielding the highest percentage was regarded as expressing the germinative capacity of the species for the year.

CLIMATIC CONDITIONS DURING THE GROWING SEASON

The seeds of the harvest of 1928 produced the highest germination for most of the species tested; those of 1929 the second highest germination. The growing season of 1928 began with low temperatures and low precipitation in April, followed by high temperatures with a continuation of low precipitation in May, before the moisture factor became critical. Low temperatures prevailed in June, so that, while the rainfall was slightly below the average for the month, drought did not occur. Average temperatures in July accompanied by high precipitation prolonged the period of growth. The temperature in August was only slightly above the mean and the rainfall was normal. In September both temperature and precipitation were below normal. During 1929 the mean temperature of April was high, that of May was low. Precipitation was average. June, July, August, and September were in general like the corresponding months of 1928, although the temperatures were slightly higher and the precipitation was somewhat lower.

The seasons of 1930 and 1931, both of which produced poor crops of seeds, were characterized by the termination of growth in midsummer because of severe drought. The excessively high temperatures in June, 1931, with rain only in heavy showers, were apparently more disastrous than the more sustained high temperatures in July, 1930. The temperatures were significant, probably, only because of their bearing on the water relation. In the shallower prairie soils moisture is frequently so near the critical point that while low temperatures may permit growth to continue, high temperatures, by increasing transpiration and evaporation, very soon result in drought. Table 4 summarizes, for the four years, the departures from the mean temperature and precipitation for each of the six months of the growing season.

TABLE 4. Mean monthly temperatures (°F.), mean monthly precipitation (in inches) and departures from the mean during 1928-1931

Year	April		May		June		July		August		September	
	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
Average of 50 years.	52	2.5	62	4.0	71	4.2	77	3.9	75	3.5	70	2.9
1928	— 4	—1.3	+ 3	—1.3	— 5	—0.3	0	+1.9	+ 1	+0.1	— 2	—0.9
1929	+ 2	+0.4	— 2	—0.8	— 1	—2.4	+ 1	+1.5	+ 2	—2.6	— 2	—1.1
1930	+ 4	+0.2	0	—0.9	0	—1.3	+ 6	—2.8	+ 2	+0.2	+ 1	—1.6
1931	+ 1	—0.8	— 3	+2.4	+ 7	+0.2	+ 3	—1.8	0	+0.3	+ 8	+0.9

DISCUSSION

It becomes apparent that the germination often varied considerably for one lot of seeds at different times of year. A species might pass out of the condition of initial dormancy which regularly follows harvest and give a large yield of seedlings from the winter planting. The following year the same species might show only low germination from the winter sowing while subsequently it produced a higher percentage, comparable to that of the preceding year; *e.g. Sporobolus asper* and *Oenothera biennis.* Further plantings in the same year might again show a reduced percentage. This might be due to return of dormancy, or, less often, to some unfavorable external condition, such as brief periods of excessive heat during tests carried on in the spring.

The majority of species were tested only once during a year, by plantings made in January and February. Work done in the course of the study indicated that it would have been better in general to have delayed sowing until 3 months later. Continuing the tests started in late winter through the spring months is not the equivalent of starting them in the spring. General correlation exists, as emphasized in commercial seed testing, between promptness

of germination and number of seedlings. This correlation is less marked in wild seeds.

Dormancy was still apparent in late winter when most of the tests were made. Species and individuals in a group of seeds of one species pass out of dormancy at different times. Such a species as *Aristida oligantha* Michx., giving a consistent, fairly high germination (30 to 40 per cent) in each planting of the three winters in which it was tested, might reasonably be assumed to have thrown off the restraints to germination. *Sporobolus asper,* on the other hand, varied in its response from year to year. The seeds of the harvests of 1928 and 1929 were mostly dormant during the winter tests. The highest germination was 7 per cent, though nearly 60 per cent was obtained a few months later. The harvest of 1930 gave 40 per cent from the February planting and a maximum of 57 in the following autumn. The forb *Salvia pitcheri* Torr. produced from the harvest of 1929, during the last half of January, a germination of 50 per cent. The next harvest, planted early in February, yielded only 15 per cent. Placed in the soil May 8 and left for three months, seeds of the same crop gave 40 per cent germination within two weeks, followed by almost complete cessation. Resumption of seedling formation during the last week of July raised the total to 61 per cent.

Relatively few of the forbs were tested except at the winter planting. In general they gave extremely poor results when sowed in summer for special tests. In several instances better germination was obtained from plantings made in the greenhouse in the spring than from winter tests. The influence of time of planting appeared to vary with species. Possibly this phase of behavior in germination, or more accurately in dormancy, is characteristic of a genus. Howard (1915) working with a large number of native species in Missouri, observed that the species of a family appeared to "show more or less the same characteristics as regards time and percentage of germination".

The general results expressed below are stated with the realization that it may not be the true germinative capacity of the seeds which is apparent, but germination restricted by dormancy.

RESULTS

Most grasses gave less than 10 per cent germination in at least one or two of the 4 years. *Agropyron smithii* remained in this group during 3 years, with percentages lying between 0.5 and 5.5. The fourth year specially selected seeds, known to contain embryos, gave 48 per cent.

Andropogon furcatus, Bouteloua hirsuta, and *Panicum virgatum* gave between 10 and 20 per cent during two of the 4 years. Their germination during the other years was lower. *Andropogon scoparius* during one year only showed a germination which was far above 10 per cent. The subclimax *Aristida oligantha* and the two weeds, *Chaetochloa glauca* Scribn. and *Pani-*

cum capillare, during both years in which they were tested, gave 20 to 40 per cent. *Bouteloua gracilis* and *Bulbilis dactyloides* (Nutt.) Raf. both produced germinations between 20 and 40 per cent during one year of the 4, between 10 and 20 during another year, and below 10 per cent during the first two years. *Elymus canadensis* always gave over 40 per cent germination and during two years over 60 per cent. The record of *Koeleria cristata* was above 40 per cent one year, between 20 and 40 during one year, and between 10 and 20 per cent during two years.

Inspection of the data (Tables 5 to 7) with the fact in mind that the winter plantings, especially during the first two years, were somewhat premature, leads to the following generalizations. A germination of 40 to 60 per cent may be expected from *Elymus canadensis*, *Poe pratensis* L., and *Sporobolus asper*. Between 20 and 40 per cent may be predicted for *Aristida oligantha*, *Chaetochloa glauca*, and *Panicum capillare*. Between 20 and 40 per cent should be induced in *Bouteloua gracilis* and *Koeleria cristata*. Koeleria is capable of giving a higher yield. Ten to 20 per cent should be obtained from *Andropogon furcatus*, *Bouteloua hirsuta* and, at least in some years, from *Andropogon scoparius*, *Bouteloua curtipendula* (Michx.) Torr., and *Panicum virgatum*. While less than 10 per cent germination was obtained from *Sorghastrum nutans*, *Spartina michauxiana*, and *Stipa spartea* during the four years of 1928 to 1931, these species are capable of giving better germination under proper conditions of seed formation, ripening and storage. Seeds of *Sorghastrum nutans* gathered in

TABLE 5. Percentage of germination of seeds of grasses of four harvests in successive tests. Percentages from unfrozen seeds are given in parentheses

Year of harvest	Year of test	Season of test	Andropogon furcatus	Andropogon scoparius	Bouteloua curtipendula	Bouteloua gracilis	Bouteloua hirsuta	Elymus canadensis	Koeleria cristata	Panicum virgatum	Sorghastrum nutans	Sporobolus asper	Spartina michauxiana
1928.....	1929	Winter.......	(2.0)	(27.5)	....	(2.5)	(11.0)	(84.0)	....	(1.0)	(5.5)	(16.5)	....
		Winter.......	2.5	37.0	5.5	3.0	7.0	81.0	26.0	2.5	8.5	6.5	....
	1930	Winter.......	5.0	11.0	....	....	2.0	....	....	....	4.0	....	....
	1931	Winter.......	.3	....	....	....	....	....	....	....	....	....	....
1929.....	1930	Winter.......	(.5)	(2.5)	(11.5)	(2.5)	(0.0)	(61.0)	(49.5)	(1.0)	(0.0)	(5.0)	(8.0)
		Winter.......	5.0	8.5	10.5	7.5	3.5	50.5	....	2.5	3.0	3.0	10.5
		Spring.......	3.0	....	....	....	10.5	....	54.0	....	....	....	....
		Summer......	19.0	....	6.0	....	....	23.0	....	....	4.0	36.0	....
		Fall.........	3.0	....	....	0.0	1.5	....	....	3.0	2.0	59.0	....
1930.....	1930	Fall.........	(1.0)	(8.0)	....	(31.0)	(5.0)	(37.0)	....	(3.0)	(6.0)	(60.0)	(0.0)
	1931	Winter.......	(1.0)	(2.0)	(0.0)	(22.0)	(10.5)	(32.0)	(29.0)	(0.0)	(1.0)	(77.0)	(3.0)
		Winter.......	4.5	.5	0.0	25.5	6.0	38.0	10.0	0.0	3.5	40.5	0.0
		Spring.......	6.0	1.5	2.5	18.0	9.0	25.5	1.5	1.0	.5	15.0	1.5
		Summer......	6.0	5.0	.5	24.0	3.5	31.0	10.0	1.5	.5	24.0	....
		Fall.........	3.5	8.0	3.5	15.0	21.5	45.5	....	11.5	4.5	57.5	1.0
1931.....	1931	Fall.........	(7.0)	(0.0)	(1.0)	(3.0)	(1.0)	(18.0)	(4.0)	(0.0)	(0.0)	(0.0)	(0.0)
	1932	Winter.......	(.5)	(4.0)	(0.0)	(6.5)	(8.5)	....	(18.0)	(1.5)	(2.0)	(3.0)	(1.0)
		Winter.......	9.0	3.0	0.0	10.5	5.5	77.9	63.0	0.0	1.0	15.5	3.0
		Spring.......	20.0	5.0	....	10.0	....	87.0	....	14.0	5.0	91.0	6.0
		Summer......	3.0	2.0	....	...	....	69.0	9.0	1.0	1.0	18.0	7.0

TABLE 6. Percentage of germination of seeds of forbs of four harvests in successive tests

Year of harvest	Year of test	Season of test	Amorpha canescens	Helianthus rigidus	Kuhnia glutinosa	Liatris punctata	Liatris scariosa	Oenothera biennis	Salvia pitcheri	Silphium integrifolium
1928.......	1928	Fall.....	(0.0)	(2.0)	(26.0)	(49.0)	(22.5)	(0.0)	....	(5.5)
	1929	Winter...	(6.0)	(10.5)	(54.5)	(39.5)	(54.5)	(36.5)	....	(28.0)
		Winter...	21.5	11.0	53.0	69.5	61.0	45.5	....	28.0
	1930	Winter...	....	....	65.0	45.5	45.0	....	....	....
1929.......	1930	Winter...	(3.0)	(11.5)	(39.0)	(51.5)	(55.5)	(55.5)	(49.0)	(12.0)
		Winter...	27.5	4.0	49.0	42.5	64.0	48.0	56.5	11.0
		Summer..	24.5	....	....	....	....	....	24.0	....
1930.......	1930	Fall.....	....	....	(45.5)	(40.0)	....	(9.0)	....	....
	1931	Winter...	(1.0)	(0.0)	(54.0)	(59.5)	(1.8)	(2.5)	(47.0)	(45.0)
		Winter...	5.0	3.5	47.0	47.0	34.5	3.5	15.0	51.5
		Spring...	8.5	2.5	57.0	41.5	25.0	58.5	61.5	47.0
		Summer..	12.0	.6	39.0	15.0	....	45.5	3.0	9.0
		Fall.....	....	....	46.0	21.0	....	....	....	....
1931.......	1931	Fall.....	....	....	(39.0)	(14.0)	(0.0)	(0.0)	....	(1.0)
	1932	Winter...	(3.5)	(1.0)	(34.0)	(62.5)	(17.0)	(2.5)	....	(2.0)
		Winter...	31.0	0.0	49.0	67.0	45.0	1.5	....	.5
		Spring...	....	....	55.0	83.0	....	13.0	....	....
		Summer..	....	0.5	17.0	30.0	6.0	17.0	....	....

1926 and stored for two years before any tests were made consistently gave germinations lying between 15 and 25 per cent during four consecutive years. *Stipa spartea,* from the harvest of 1926, tested in its third year, gave 50 per cent. The germination from *Spartina michauxiana* was always small. With the exception of two plantings it gave less than 5 per cent.

The forbs as a whole showed higher germination from the harvests of 1928 and 1929 than from those of 1930 and 1931. This was the more conspicuous because practically the only tests made during the first two years were those of the regular winter plantings. The percentage from the two later harvests were sometimes increased by additional tests in the spring. The highest figure obtained from all tests of dried and frozen seeds during a year was regarded as expressing the germination for a given harvest.

Species giving over 40 per cent germination at least two years, and usually three out of four seasons, included *Anemone cylindrica* A. Gray, *Kuhnia glutinosa, Liatris punctata, L. scariosa, Oenothera biennis, Physalis lanceolata* Michx., *Tragopogon pratensis* L., and *Salvia pitcheri.* Both Anemone and the ruderal Tragopogon produced germinations of more than 90 per cent from one of the harvests. Physalis gave a maximum of 83 per cent. Kuhnia showed a maximum of 65, with a frequent germination of 50 per cent. *Liatris punctata* produced a maximum of 83 per cent, though its germination was usually between 50 and 70 per cent. *Liatris scariosa* showed the same range. The maximum, 81 per cent, was obtained from a harvest previ-

TABLE 7. Percentages of germination of seeds of four harvests, tested once only. Percentages from unfrozen seeds are given in parentheses

Year of harvest	1928	1929	1930	1931
Year of test	1929	1930	1931	1932
Agropyron smithii	(11.5)	(1.0)	(0.0)	(6.0)
	5.5	2.5	.5	49.0
Aristida oligantha	(23.0)	(44.0)	(25.5)	....
	39.5	42.0	30.5	....
Bulbilis dactyloides	(8.0)	(10.5)	(14.0)	(2.5)
	7.0	14.5	33.0	5.5
Chaetochloa glauca	(37.5)	(7.5)	....	....
	38.0	22.5	....	...
Panicum capillare	(27.0)	(5.0)	....	....
	23.5	40.5	....	...
Stipa spartea	...	(4.3)	(3.2)	(2.5)
	....	8.0	3.0	0.0
Carex festucacea	....	(.5)	(0.0)	....
	....	.5	.5	.5
Achillea occidentalis	....	(2.7)	(29.0)	(18.5)
	....	7.5	36.0	24.0
Anemone cylindrica	(70.5)	.	(15.5)	...
	91.0	49.5	10.0	...
Antennaria campestris	....	(4.5)	(8.0)	(4.0)
	....	0.5	3.0	3.5
Artemisia gnaphalodes	(12.5)	(0.0)	(0.0)	(0.0)
	21.0	0.0	0.0	0.0
Aster multiflorus	(1.0)	(.5)	(0.0)	(5.5)
	9.0	7.0	.5	.5
Aster salicifolius	(8.0)	(3.0)	(0.0)	(10.0)
	9.5	3.0	1.0	5.5
Astragalus canadensis	(.5)	(5.0)	....	....
	2.5	2.0	3.5	.
Echinacea pallida	(3.5)	(3.5)	(3.5)	(1.0)
	1.5	7.0	5.0	1.5
Glycyrrhiza lepidota	(0.0)	(1.0)	(1.0)	....
	1.0	2.0	.5	....
Grindelia squarrosa	(35.5)	(11.5)	(9.5)	....
	50.0	9.5	17.0	....

Year of harvest	1928	1929	1930	1931
Year of test	1929	1930	1931	1932
Hieracium longipilum	....	....	(10.0)	(53.0)
	2.8	....	24.5	18.5
Lespedeza capitata	(1.0)	(2.5)	(0.0)	(0.0)
	3.5	4.0	0.0	0.0
Meibomia illinoensis	(8.5)	(3.5)	(13.0)	(3.5)
	46.0	7.0	21.0	17.5
Petalostemon spp.	....	(2.5)	....	(.5)
	....	12.5	9.0	7.0
Physalis lanceolata	(76.5)	(59.5)	(47.0)	(14.5)
	83.5	67.0	48.0	19.5
Rosa arkansana	(.5)	(0.0)	(0.0)	(0.0)
	0.0	0.0	0.0	0.0
Silene antirrhina	....	....	....	....
	....	69.3	47.0	....
Silphium laciniatum	...	...	(31.0)	....
	....	0.0	45.0	....
Silphium perfoliatum	...	....	....	....
	...	8.8	50.0	....
Sisyrinchium angustifolium	...	(0.0)	....	(0.0)
	....	....	2.0	0.0
Solidago altissima	(1.5)	...	(0.0)	(1.0)
	3.0	12.0	1.3	0.0
Solidago glaberrima	....	(6.0)	....	(0.0)
	....	12.0	...	.5
Solidago rigida	(4.0)	(16.5)	(0.0)	....
	6.0	15.0	.5	....
Tragopogon pratensis	...	(74.0)	(71.0)	(58.5)
	....	95.0	70.5	54.0
Verbena stricta	(2.0)	(3.0)	(.5)	(0.0)
	3.0	6.5	.5	0.0
Vernonia baldwini	(26.0)	(30.0)	(2.5)	(0.0)
	15.0	11.0	11.5	1.0

ous to the collections of this study, tested after 3.5 years of dry storage. *Oenothera biennis* gave a maximum of 58 per cent. Usually the germination was 45 to 50 per cent. *Amorpha canescens* Pursh gave about 30 per cent in the tests of two years, somewhat over 20 per cent one year and 12 per cent after the hot summer of 1930. *Meibomia illinoensis* (A. Gray) Kuntze produced 46 per cent during one year, about 20 per cent in the tests of two other years and less than 10 per cent from its poorest harvest. *Grindelia squarrosa* (Pursh) Dunal varied from 10 to 50 per cent during three years of testing. Silphium spp. produced 45 to 50 per cent as maximum germination. The yields from the rosin weeds were small, owing to irregularity of germination, unless they were left in the soil for a period of six months or more. *Achillea occidentalis* Raf. gave percentages of 36 and 24 in two of the three tests. The third harvest, collected very late in the season, gave less than 10 per cent.

Artemisia gnaphalodes Nutt. produced 21 per cent of seedlings from the harvest of 1928. The three later crops failed to germinate. Few seeds could be found in the dried flower heads. *Vernonia baldwini* Torr. showed germinations of 10 to 15 per cent during three years out of four. Three species of goldenrod, *Solidago altissima* L., *S. rigida* L., and *S. glaberrima* Martens (tested two years only) gave germinations of 12 to 15 per cent from the harvests of 1929. Usually the percentage was less than five. *Helianthus rigidus* (Cass.) Desf. produced 11 per cent from the seeds of 1928 and less than 5 per cent during other years. Two species of Petalostemon gave about 10 per cent in several tests. Less than 10 per cent was obtained in any season from *Aster multiflorus* Ait. (*A. ericoides* L.), *A. salicifolius* Lam., *Echinacea pallida* (Nutt.) Brit., and *Verbena stricta* Vent.; less than 5 per cent from *Antennaria campestris* Rydb. and *Astragalus canadensis* L. (*A. carolinianus* L.). *Lespedeza capitata* Michx. gave less than 5 per cent, except from a test of seeds gathered two years previous to the beginning of this experiment. These, tested after two and one-half years of storage, yielded 14 per cent. *Glycyrrhiza lepidota* Nutt., *Rosa arkansana* S. Wats. (*R. suffulta* Greene), and *Sisyrinchium angustifolium* Mill. (tested two years) did not exceed two per cent (Tables 6 and 7).

CONCLUSIONS

Most prairie species produce large numbers of seeds. Small but by no means negligible percentages of these are viable. The number of seedlings obtained varies greatly with the growing season preceding the harvest. Species producing seeds which give germinations of 50 to 80 per cent when grown in relatively cool, moist summers, are greatly handicapped in seed formation during the more frequent seasons characterized by periods of drought. The same species, particularly if drought occurs before mid-summer, may produce seeds which give a germination of less than 20 or even less than 10 per cent.

The time of year when a test is made is an important factor for seeds in which it is hard to break dormancy. A given lot of seeds which produces extremely low germination or none from a single test may yield much better results at a more favorable time. The spring, particularly April and May, has been found to be the season when native prairie seeds produce seedlings most readily and abundantly. Early fall of the year subsequent to that of the harvest proved to be second only to spring, and occasionally more favorable, as a season for germination. Once the seeds are thoroughly ripened, some species seem to be almost as dependable as cultivated crops; *e.g. Bouteloua gracilis, Sporobolus asper, Amorpha canescens,* and *Salvia pitcheri.*

The seeds of most prairie plants are subject to deep dormancy during the greater part of the year. Wild seeds, however, are far less certain than those of cultivated species to be killed by subjection to conditions conducive to

germination at times unfavorable for development. They often remain latent, no doubt with somewhat lowered vitality. While many die, a surprisingly large number will develop if conditions again become suitable during the season which is normal to them for germination.

Relative Germination of Frozen and Unfrozen Seeds

Two hundred frozen and 200 unfrozen seeds of each species were planted in the winter tests of germination. The duplicate lots of 100 seeds each were sowed at the same time.

RESULTS

Slight but probably definite superiority in germination was observed, during tests of 3 or 4 consecutive years, from frozen seeds. Inconsistencies were common from season to season, so that the results from a single year would not have been a safe criterion of the influence of freezing. In comparisons of the germinations following the 2 treatments of stored seeds (Tables 5 to 7) differences of more than 5 per cent have been regarded as large; 5 to 2 per cent as small, and under 2 per cent as insignificant.

Andropogon furcatus and *Bouteloua gracilis* alone, of 13 grasses tested through 4 consecutive years, always produced higher germination from frozen than from unfrozen seeds. The differences were never large. Five species gave higher germination from frozen than from unfrozen seeds during 3 years out of 4 or 2 years out of 3: *Agropyron smithii, Aristida oligantha, Panicum virgatum, Sorghastrum nutans,* and *Spartina michauxiana.* The excess of seedlings from unfrozen seeds, which occurred in one year only, was small except for *Agropyron smithii. Andropogon scoparius* produced distinctly higher germination from frozen seeds of 1928 and 1929 and slightly lower germination from frozen seeds of 1930 and 1931.

Frozen seeds of several forbs always produced more seedlings than unfrozen seeds. Such species were *Achillea occidentalis, Amorpha canescens, Lespedeza capitata, Liatris scariosa,* species of Petalostemon and *Physalis lanceolata.* The advantages of frozen seeds were always large for these species with the exception of *Lespedeza capitata. Antennaria campestris* only among the forbs consistently gave higher germination from unfrozen seeds. The germination of this species was always low. When forbs produced a higher yield from unfrozen seeds, the difference was small or insignificant in twice as many instances (20 specific cases) as it was large.

DISCUSSION

While only the winter sowing was made to test the unfrozen crops, the frozen seeds were planted, in many species, two to several times during one or more years. The percentage differences shown by one species in successive tests during a year often exceeded the differences between frozen and

unfrozen seeds. Many seeds at least during some years, had not completed ripening by late winter or were still in a condition of deep dormancy. *Oenothera biennis* furnished a clear example of this. Seeds of 1928, planted January 31, 1929, gave little germination until March. Between the middle of March and the last of May they gave a total germination of 45.5 per cent from the frozen seeds and 36.5 from the unfrozen. The seeds of 1929, planted January 14, began to germinate late in February. By the middle of April the frozen seeds had produced 48 per cent germination and the unfrozen 55.5. By fall they had returned to the dormant condition, as at that time they gave only 3 per cent.

The unfrozen seeds of Oenothera varied in general with the annual fluctuations of the frozen seeds planted at the same time. The first two years the yields of both were high; the last two years the winter yields were very low.

In a few instances freezing seemed to have a distinctly injurious effect. Seeds of *Hieracium longipilum* Torr. from the harvest of 1931 when unfrozen yielded 53 per cent germination; after freezing, 18.5. The preceding year, on the other hand, the unfrozen percentage was 10 and the frozen exceeded 20. Among grasses, *Elymus canadensis* and *Sporobolus asper* sometimes showed, when sown in winter, distinctly better germination from unfrozen than from frozen seeds. No external irregularity in conditions could be observed to account for such inconsistencies.

CONCLUSIONS

Freezing of seeds in dry storage probably tends to accelerate the processes which cause a seed to break dormancy and respond to conditions favorable to growth (Pack, 1921). This is indicated by a somewhat higher percentage of germination from seeds which have been exposed, in a dry condition, to winter temperatures of 20 to 32°F. for several weeks, compared with seeds which have been kept for the same length of time at room temperatures (60°F. and usually above). For a few species distinct improvement could be seen. The increase, however, was seldom large enough or consistent enough to be of unquestionable significance.

Length of Period of Dormancy After Planting

The interval between the planting of seeds and the appearance of seedlings above ground shows much variation in any native species. The latent periods have been computed mainly from the winter tests, though comparisons have been made with the incubation time shown by plantings at other seasons. The number of days between the date of sowing and the approximate date on which the largest proportion of new seedlings appeared has been considered more important than the time of the first germination. The time of the last germination is probably relatively insignificant. Almost any lot of

wild seeds contains a few members which resist development for a long while and finally germinate if left in moist ground for many weeks.

The latent period varies with the condition of the seed. Within a species, an abnormally long interval before germination usually accompanies the production of a low percentage of seedlings. The period of dormancy in the soil is generally shorter in the last half of the spring than in winter or in midsummer.

RESULTS

A definite latent period was found for the seeds of only a few species. The largest number of seedlings of a given species usually appeared in practically the same number of days from both frozen and unfrozen seeds. In one or occasionally 2 years out of 3 or 4, a few grasses and a considerably larger number of forbs showed a much briefer period of dormancy for frozen than for unfrozen seeds. Less than a third as many instances were recorded of briefer dormancy of unfrozen seeds. In most of these instances, the larger number of seedlings was produced from the type of storage characterized by the shorter latent period.

The seeds studied have been grouped into four classes of rather wide range in respect to incubation period in the soil. Exceptions to all of these groups occur. The time applies to plantings made at fairly appropriate seasons of the year. Favorable conditions, either external or internal, may greatly shorten the dormancy for a few seeds of any species.

Species germinating in less than two weeks include the greater number of the grasses tested: *Andropogon furcatus*, Bouteloua spp., *Bulbilis dactyloides, Chaetochloa glauca, Elymus canadensis, Koeleria cristata, Panicum capillare, Poa pratensis,* and *Sporobolus asper*. Most of the forbs were about equally divided between the group which germinated within 2 weeks and the group which required between 2 and 4 weeks. Those germinating in less than 2 weeks included *Achillea occidentalis, Amorpha canescens, Astragalus canadensis, Grindelia squarrosa, Hieracium longipilum, Kuhnia glutinosa, Liatris punctata, Oenothera biennis, Salvia pitcheri,* and *Tragopogon pratensis.* Most of the species of this group were capable of giving good germination within ten days.

Species requiring from 2 to 4 weeks for germination included *Agropyron smithii, Andropogon scoparius, Aristida oligantha, Panicum virgatum,* and *Sorghastrum nutans,* and a much larger number of forbs. The latter were represented by *Antennaria campestris, Aster salicifolius, Echinacea pallida, Glycyrrhiza lepidota, Helianthus rigidus, Lespedeza capitata, Meibomia illinoensis,* Petalostemon spp., *Physalis lanceolata,* Salidago spp., and *Vernonia baldwini.*

Species producing most of their germinations between 4 and 6 weeks after sowing included the two grasses *Spartina michauxiana* and *Stipa spartea*

and the forbs *Anemone cylindrica, Aster multiflorus,* and *Verbena stricta. Liatris scariosa* usually occurred in this group in the winter plantings. It always required considerably more time than *L. punctata.*

Species requiring more than six weeks in the soil before germination became abundant included 3 species of Silphium. *Artemisia gnaphalodes,* in the one year in which it germinated, appeared in the same group. The rosinweeds were characterized by irregularity in time of germination. At the end of the usual 3 month tests they were beginning to develop somewhat freely. The seeds of the harvest of 1930 were left in the ground for a period of 8 months, from late winter to mid-fall. Under careful watering seedlings appeared, a few at a time, throughout the summer and the first half of September. Germination of 3 species of Silphium was increased from 10 to 18 per cent at the end of 3 months to totals of 45 to 50 per cent. No definite period could be marked off as the time during which the largest number of germinations occurred.

CONCLUSIONS

The length of the latent period for seeds planted in soil varies greatly with the season of planting. If this is favorable, most grass seeds will germinate within 2 weeks. Most of the forbs belong to one of two groups of about equal numbers: those which germinate in less than 2 weeks and those which require 2 to 4 weeks. A few species of both grasses and forbs seldom produce many seedlings until the second month after planting.

GERMINATION OF SEEDS FROZEN IN MOIST SOIL

The effect of freezing seeds planted in moist soil was tested for 15 grasses, one sedge and 26 forbs, all from the harvest of 1931. The experiment was started in the early winter of 1931 and continued through the following spring. Two years later the experiment was supplemented by a repetition with 7 species of grasses and 10 of forbs from the harvest of 1933.

METHODS

The seeds were dried in the air and stored indoors until December. They were then planted in duplicate lots of 100 each. Plantings were made in large flats filled with screened prairie soil of good water content. The seeds were covered with a layer of earth of a thickness equal to about 4 times their diameter. This was pressed firmly over them and well watered, to insure contact of the seeds with a supply of moisture. The flats were covered with cheesecloth to prevent entrance of foreign seeds and placed out-of-doors until the end of the experiment. Records of germination were kept until June.

RESULTS

Nearly all of the germination occurred during April. At the first observation, April 5, many very young plants were present. In the majority of

the species they formed relatively large, even stands. This was conspicuous for several species characterized in the greenhouse by very uneven development. Examples were rosin-weed with 50 seedlings in one of the duplicate lots and 68 in the other; two species of goldenrod with 15 to 20 in each lot; and tall marsh grass with 4 in one duplicate and 11 in the other. Very little germination occurred after May 5. Amorpha and Meibomia constituted exceptions, with about half of the seedlings of each appearing between May 5 and 19.

Higher germination under stratification than from either frozen or unfrozen dry storage was given by 7 of the 14 species of grasses. The percentages were 2 or 3 times as large as maxima for the year obtained from dry storage. The percentage germinations from stratification and from seeds stored dry were respectively: *Andropogon scoparius*, 11 and 5; *Bouteloua curtipendula*, 5 and 0; *B. hirsuta*, 21 and 8; *Bulbilis dactyloides*, 35 and 6; *Koeleria cristata*, 58 and 18; *Spartina michauxiana*, 12 and 7; *Stipa spartea*, 9 and 3 per cent. Fewer seedlings were produced from stratification than from dry storage by *Andropogon furcatus* (13.5 as against 20 per cent), *Bouteloua gracilis* (6.5 and 10.5), *Elymus canadensis* (55.5 and 87), *Poa pratensis* (57.5 and 78.5) and *Sporobolus asper* (83 and 91). *Panicum virgatum* (14 per cent), and *Sorghastrum nutans* (5 per cent) gave maximum germination from dry storage equal to that from stratification. *Carex pennsylvanica* Lam. increased in germination from 0.5 for seeds frozen dry to 3 per cent for those which were layered.

In the supplementary experiment 6 of the 7 species of grass gave distinctly higher germination under stratification than without it. The seventh yielded practically the same by both methods. The three which agreed definitely with the results of the original experiment were *Bouteloua hirsuta* (11 per cent stratified; 8, not stratified), *Bulbilis dactyloides* (42, stratified; 3, unstratified), and *Spartina michauxiana* (46, stratified; 21, not stratified). *Panicum virgatum* and *Sorghastrum nutans*, which had showed no improvement in the previous experiment, increased markedly under stratification, the panic grass from 2 to 8 per cent and the Sorghastrum from 45 to 60. *Andropogon furcatus*, contrary to the effect obtained earlier, produced twice as much germination under stratification (15 per cent, compared to 7 per cent without it). *Andropogon scoparius*, which had formerly improved in yield under stratification, gave 18 per cent stratified and 19 per cent after dry freezing.

Twenty of the 26 species of forbs in the first test gave distinctly higher germination from the seeds which lay in moist soil out-of-doors all winter than from those which were stored dry. The percentage from stratified seeds was usually 2 or 3 times higher and often much more. *Achillea occidentalis*, for example, increased from 27 to 63 per cent; *Antennaria campestris* from 4 to 9; *Aster multiflorus* from 5 to 10; *A. salicifolius* from 10 to 28;

Echinacea pallida from 2 to 38; *Helianthus rigidus* from 1 to 19.5. Two species increased slightly: *Erigeron ramosus* (Walt.) B. S. P. from 10 to 12 and *Rosa arkansana* from 0 to 0.5 (differences too small to be significant). *Lespedeza capitata* increased from 0 to 4 per cent; *Petalostemon candidus* (Willd.) Michx. from 9 to 17; *Physalis lanceolata* from 19 to 73; *Psoralea floribunda* Nutt. from 9 to 24; *Silphium integrifolium* Michx. from 2 per cent, at the end of the 3-month incubation period of the winter test, to 65 per cent; *Solidago altissima* from 1 to 22.5 per cent; *S. glaberrima* from 0.5 to 37; *Vernonia baldwini* from 1 to 44. Three species which gave no germination from either type of dry storage produced good or high percentages from stratification: *Pentstemon grandiflorus* Nutt., 35 per cent; *Sisyrinchium angustifolium*, 17; *Verbena stricta*, 53. All 3 species in previous years had given very little germination or none.

Four forbs produced lower germination under stratification than from either kind of dry storage. *Hieracium longipilum* was reduced from 53 per cent (unfrozen) and 18 (dry frozen) to 0 per cent when layered. *Kuhnia glutinosa* was reduced from 55 per cent from dry frozen storage to 22 when layered, and *Liatris punctata* from 83 to 26. *Tragopogon pratensis* showed slight differences in germination: 58 per cent from unfrozen seeds, 54 from those which were frozen dry, 53 from stratification. *Liatris scariosa*, with a maximum germination of 45 per cent from dry frozen seeds, decreased under stratification to 29 per cent. *Amorpha canescens* also decreased in yield, from 31 per cent after dry freezing to 17 from stratified seeds.

The supplementary stratification of 10 forbs two years later greatly increased the germination of 6 species and produced little or no apparent change in the seeds of 4 species. No significant decreases were observed. The same degree of improvement noted the first year was obtained in the second test of *Physalis lanceolata* (69 per cent with stratification and 12 per cent without it), *Verbena stricta* (20 per cent with it and 7 without) and *Vernonia baldwini* (42 and one per cent respectively). *Solidago canadensis* increased to 11.5 from 0 under the treatment. *S. altissima*, however, which had increased from one to 23 per cent in the first stratification experiment, yielded 29 per cent from dry freezing and dropped slightly to 27 per cent when stratified. *Aster multiflorus*, which had increased from 5 per cent to 10 in the first stratification, made an insignificant rise in negligible germination from 0 to 0.5. *Amorpha canescens* also gave too small germination by both methods (between one and 2 per cent) to be considered. *Helianthus rigidus*, which had risen from one to 19.5 when stratified after the previous harvest tested, gave equal yields of 17 per cent. Two closely related composites which had appeared to be seriously injured by freezing in the ground underwent as great a change, in the supplementary experiment with a subsequent harvest, in the opposite direction; *Kuhnia glutinosa* (60 per cent,

stratified and 25, non-stratified) and *Liatris scariosa* (63 stratified, and 36, not stratified). No other forbs were tested.

DISCUSSION

In considering the effect of stratification, the first problem is to determine the germinative capacity of a species under dry storage. The highest percentage obtained at any time during a year has been regarded as the germinative capacity for that year. Owing to fluctuations shown by most species in the course of a year, it is impossible to be certain of the potential germination from the numbers of seedlings observed. The maximum from the entire four years of the study probably constitutes the best basis obtainable from these data for estimating the germinative power of a species. Comparison of the results of stratification have been made, accordingly, with the two highest records of each species during the entire period of work.

The harvest of 1931 from which stratified seeds were taken was in general poor and resulted in low germination from dry stored seeds of many species. The percentages from stratified seeds may have been lower also than if they had been from another harvest. There is some evidence, however, that stratification tends to improve the germinating power of poor seeds more than that of good ones. Conspicuous improvement under stratification was observed for several species which were making unusually low records from that particular harvest after dry storage; *e.g.* *Andropogon scoparius* in the first year, *Panicum virgatum* in the second, *Bulbilis dactyloides* during both seasons, *Achillea occidentalis* and *Silphium integrifolium* during the first test. *Helianthus rigidus* from the harvest of 1931 produced consistently the lowest germinations obtained from the species (from one to zero per cent). Stratified, however, the seeds of this crop gave the maximum for the species, 19.5 per cent. The harvest of 1933, on the other hand, produced a distinctly higher germination of seeds frozen in dry storage than the crop of any other season studied. This percentage (17) was not altered under stratification. *Physalis lanceolata,* ordinarily very prolific of seedlings, gave from the dry stored seeds of 1931 an extremely low record (20 per cent, contrasted with 48, 67, and 83 of the 3 previous years). The stratified seeds, however, from this apparently poor crop germinated 73 per cent. The supplementary test with seeds of 1933 showed improvement of similar magnitude over low germination of dry frozen seeds (from 12 to 69 per cent). The stimulus of cold for a period of 3 or 4 months on the well moistened seeds more than compensated, apparently, for the condition of development which they had attained at the time of harvest. Temperatures slightly above freezing (not actually freezing) are regarded as essential for the chemical and physical changes which characterize stratification (Davis and Rose, 1912; Eckerson, 1913). In most instances freezing does no harm.

Stratification produced more striking improvement in the seeds of forbs,

on the whole, than in those of grasses. The largest increases were in species which usually yielded very low percentages. The germinations from stratified seeds appeared in April and to a less extent in May, months which sometimes displayed improvements in the records of species producing few seedlings when planted in winter. The increase, however, was very small compared to that which followed stratification. Germination of *Verbena stricta* of 1931, which was 0.5 in both winter and spring tests and below 7 per cent for maximum germination during the 4 years, increased to 53 per cent after stratification. The repetition test of this species with the harvest of 1933 was less conspicuous. Dry freezing was followed by a germination of 7 per cent, stratification by one of 19.5 per cent.

One grass only underwent improvement comparable to that shown by several forbs. *Bulbilis dactyloides* produced out of the harvest of 1931 a germination of 6 per cent from seeds frozen dry and 35 per cent from stratification; out of the harvest of 1933 a germination of 3 per cent from dry freezing and 42 per cent from stratifying. The highest germination obtained during the entire study for this species and for *Sorghastrum nutans* and *Spartina michauxiana* came from stratified seeds. The remarkably large figures for Spartina from the 1933 crop (20 per cent without stratification, 46 per cent following it) were due to the selection of seeds for the presence of embryos by the aid of electric light, as described for the final germination test of *Agropyron smithii.*

Koeleria cristata after stratification of the seeds of 1931 gave very nearly the highest germination obtained for the species, 58 per cent. It greatly exceeded the yields from the test made in late winter. A test of the same harvest, however, made in early January, produced a germination of 63 per cent, almost entirely between 10 and 14 days after the sowing.

Stratified seeds of *Stipa spartea* of 1931 produced a germination of 9 per cent, surpassing that of seeds planted in the greenhouse 7 or 8 months after being harvested. The actual maximum, however, was from unfrozen seeds of the same crop. This largest yield was from a planting of 100 seeds in the garden June 20, shortly after they had been collected. After lying in the ground 7 to 8 weeks they began to germinate. In the following 6 weeks they produced a stand of 19 seedlings. In the season under consideration this would have been impossible except for artificial watering.

CONCLUSIONS

Stratification of seeds of grasses through the winter months resulted generally in higher germination than was otherwise obtained from a given crop. As the harvests of only one or two seasons were tested for the effect of stratification, the results were not entirely conclusive. The maximum germination of 3 to 5 harvests was obtained, for most species, from seeds frozen in dry storage.

Stratification of seeds of forbs resulted, for the majority of species tested, in maximum germination greatly in excess of the percentages from all harvests stored dry, either unfrozen or frozen.

Stratification makes germination more independent of the season of sowing and less sensitive to variations in external conditions (Joseph, 1929). Many fluctuations in environment, adequate to arrest development of seeds from dry storage, are no deterrents immediately after stratification. Sometimes seedling production after thorough ripening in dry storage was found to be as high as that which followed stratification. More often, however, the output of dry-stored seeds was reduced by one or several of the conditions operating at the time of the test.

Seeds kept permanently dry, at temperatures well above freezing, experience the same chemical and physical changes, before they cease to be viable, which constitute the advantages of stratification (Flemion, 1933). Seeds tested, in the course of this study, at intervals during six years of dry storage yielded, in several instances, higher germination than the same species of the current year, or the same species under stratification. The difficulty in planting a crop of dry seeds capable of high germination lay in determining the time when their maximum capacity could be realized.

As several recent investigators have pointed out, the advantages of stratification are often lost when the seeds are transferred to dry storage at relatively high temperatures. If the chemico-physical changes which must precede germination are reversible in nature, altered external conditions may readily cause the reestablishment of dormancy. The structures, single or combined, which are instrumental in preventing germination, differ with the kind of seed. Most often the obstruction has been found in some part of the seed coat. Davis (1930), working on the seeds of *Ambrosia trifida,* demonstrated that a cold, moist medium, surrounding the seed, increased the permeability of the nucellar membrane to oxygen. Subsequent exposure to dry heat reduced the permeability and resulted in secondary dormancy.

Seeds planted in moist soil and left out-of-doors during winter complete the changes which must precede germination more quickly than in dry storage. As they are in the soil in early spring, they are able to develop into seedlings before the external medium becomes so hot or so dry as to induce chemical activity of an opposing nature. Air-ripened seeds, after passing through the same changes, are less likely to be held in the stage which is essential for germination until external conditions become favorable for development.

There is not much danger that native seeds will germinate prematurely in the ground during unseasonable warm periods in winter. September or October plantings might germinate to some extent in the fall. To obtain early and abundant germination in a given area out-of-doors in the spring,

very late fall sowing would appear to be essential for most forbs and advantageous for most grasses.

Optimum Water Content of Soil for Germination

Tests were made to determine the degree of soil moisture most favorable for germination. Such a determination is practically useful in germinating seeds in the greenhouse and is suggestive in considering the factors influencing seedling production under natural condition.

METHODS

Selection was made of several grasses and forbs which grow in locations characterized by considerable differences in soil moisture. Seeds were planted only in soil of such water content as they would be likely to encounter in nature.

The soil was a silt loam with a hygroscopic coefficient of 7.6, a water-holding capacity of 55 per cent and a pH of 7.7. The degrees of constant water content used were saturation, and percentages which produced approximately 2/3, 1/2, and 1/3 saturation. In addition three species were tested in soil of somewhat less than 1/5 saturation. As a control, all species were planted in soil which was alternately well watered and allowed to become quite dry.

The tests were made in deep, open pans, covered with glass plates and sealed with vaseline. Two kilograms of dry soil were placed in each pan. The required amount of water was thoroughly mixed with the soil for low percentages of saturation. For higher percentages, part of the water was mixed with the soil. The remainder was added very gradually and the soil was allowed to stand 2 or 3 days before planting, in order that equilibrium might be attained. Otherwise the soil structure was destroyed and the air more or less completely displaced.

For each species, equal, measured amounts of seeds were planted in the soil of various degrees of water content. Somewhat over 100 seeds of large size and about 300 seeds of very small size constituted a planting. Germination was expressed by numbers of individual seedlings which appeared. The plantings were made early in May. The experiment was continued through a period of 6 weeks.

SPECIES TESTED

Eight species of grasses and 4 of forbs germinated in sufficient numbers to be considered. Two species of Andropogon, two of Bouteloua, *Elymus canadensis, Koeleria cristata, Panicum virgatum,* and *Spartina michauxiana* composed the list of grasses. The forbs were *Amorpha canescens, Petalostemon candidus, Salvia pitcheri,* and *Solidago glaberrima.* All were planted in soil of 1/3, 1/2, and 2/3 saturation and in soil which was alternately wet and dry. *Andropogon scoparius, Bouteloua curtipendula,* and *Amorpha canes-*

cens were planted also in soil of about 1/5 saturation. Four species of grasses and one forb were planted in saturated soil: *Andropogon furcatus, Elymus canadensis, Panicum virgatum, Spartina michauxiana,* and *Salvia pitcheri.*

RESULTS

One-third saturation proved to be distinctly the optimum for *Amorpha canescens. Petalostemon candidus* also germinated better in one-third saturation than in any other degree of constant water content. Its maximum germination, however, occurred in soil which was alternately wet and dry.

One-half saturation proved to be optimum for *Bouteloua curtipendula, Koeleria cristata,* and *Salvia pitcheri. Bouteloua curtipendula* produced considerable numbers of seedlings in all degrees of moisture, even one-fifth saturation. It was the only species which germinated in such dry soil. The seeds were from plants grown in a garden, as the harvest of this species secured on the prairie during the preceding summer yielded practically no germination. *Koeleria cristata* produced good germination in 1/3 saturation, while *Salvia pitcheri* gave none.

Two-thirds water content was optimum for 3 grasses: *Andropogon scoparius, Elymus canadensis,* and *Spartina michauxiana. Elymus canadensis* gave very poor germination for a species which usually grows so readily. Neither this species nor Spartina germinated under complete saturation.

Equally good germinations in both 1/2 and 2/3 saturation were recorded for *Andropogon furcatus, Panicum virgatum,* and *Solidago glaberrima. Andropogon furcatus* showed the most uniform germination of any species tested, judged by both numbers of seedlings and latent periods. Even under saturation 2 germinations occurred at the end of 10 days. This was the only species which germinated in a saturated medium. *Panicum virgatum,* which usually produced a negligible percentage, gave a germination probably too small to be significant. The details of the numbers of seedlings and the latent period of greatest amount of germination in each group are given in Table 8.

DISCUSSION

The quality of the seeds must be taken into consideration in interpreting the results of such an experiment. The inferiority of seeds raised under adverse conditions may permit them to germinate only where water content is optimum. The superior osmotic and imbibitional power of well developed seeds may considerably extend their range of germination. The optimum for a species would probably be constant. The limits from which germination might be expected would vary with the harvest.

The maintenance of a proper balance between water supply and oxygen supply determines the water content of soil which is optimum for germination. Alternate wetting and drying improve aeration over that of soil of constant moisture. The danger lies in the probability that, after a seed has

TABLE 8. Relation of germination to soil moisture

Species	Germination	1/3 sat.	1/2 sat.	2/3 sat.	Alternately wet and dry
Andropogon furcatus	No. of plants	6	9	10	8
	Time (days)	7	7	7	10
Andropogon scoparius	Plants	15	16	18	11
	Time	13	11	11	20
Bouteloua curtipendula	Plants	65	81	37	49
	Time	14	5	5	9
Bouteloua gracilis	Plants	4	4	3	5
	Time	8	4	4	7
Elymus canadensis	Plants	1	7	16	9
	Time	24	27	10	24
Koeleria cristata	Plants	161	261	59	25
	Time	8	8	4	14
Panicum virgatum	Plants	0	1	1	1
	Time	..	7	7	7
Spartina michauxiana	Plants	0	0	3	1
	Time	..	..	37	31
Amorpha canescens	Plants	92	36	17	22
	Time	6	6	6	6
Petalostemon candidus	Plants	31	27	6	44
	Time	10	4	4	7
Salvia pitcheri	Plants	0	21	14	17
	Time	..	4	4	10
Solidago glaberrima	Plants	0	5	5	0
	Time	..	4	4	..

initiated germination and its protoplasm has been converted into the unstable, sensitive state, subsequent drying will injure it. It may be killed, or it may merely be reduced again to a dormant condition. In either event no seedling will be produced. When a seed germinates quickly enough to avoid drying, it takes the first step in increasing the establishment of its species. Whether or not young plants will survive long enough out-of-doors to be seen, even if they have succeeded in germinating, will depend on the rapidity with which their seminal roots penetrate the generally moister layers below the level of the seed.

CONCLUSIONS

Two-thirds saturation was the optimum constant water content for germination for species characteristic of the more moist parts of the prairie. One-third to one-half saturation was the optimum of constant water content for most species of dry areas. For species which germinated very quickly, the optimum was sometimes furnished by alternate wetting and drying.

GERMINATION IN PRAIRIE SOD

Germination in prairie sod kept under favorable conditions of temperature and moisture in the greenhouse was studied during 4 years, from 1928 to 1931. Half of the lot of sod was frozen out-of-doors before germination was permitted to occur.

METHODS

Sod was removed from the prairie about November 1, after most of the seeds had fallen but before the ground became frozen. It was cut to a depth of 4 inches and fitted into flats carried into the field. The surface area was about 20 square feet, except that the amount collected the first year was considerably smaller. Two flats were filled at each location selected, so that duplicate sets were obtained. One of these was placed in the greenhouse immediately and kept under conditions favorable to germination. The other was well watered, covered with cheesecloth to prevent the entrance of seeds, and left out-of-doors until the middle of February. It was then brought into the greenhouse to induce germination. Inspection was made at intervals of 2 to 4 weeks for the appearance of seedlings.

All collections were from the interior of a square mile of unbroken prairie 9 miles northwest of Lincoln, except a part of the samples taken in 1928. These were from the less isolated Belmont prairie, directly north of Lincoln, and afforded the large number of weedy grasses which appeared during the first year.

RESULTS

Germination varied widely from year to year both in species and in numbers of individuals. Only 4 grasses and 4 forbs were represented during each of the 4 years. These were *Koeleria cristata, Panicum scribnerianum* Nash, *Poa pratensis, Erigeron ramosus, Linum sulcatum, Oxalis stricta,* and the ruderals, *Panicum capillare* and Lepidium spp. Five other grasses and 3 forbs appeared during each of 3 years. These included *Andropogon furcatus, Elymus canadensis, Festuca octoflora* Walt., *Senecio plattensis,* and the weedy plants, *Bromus tectorum* L., *Syntherisma sanguinalis* (L.) Dulac, Euphorbia spp., and *Silene antirrhina* L. The number of individuals was never large except for the 4 grasses, *Bromus tectorum, Festuca octoflora, Koeleria cristata,* and *Poa pratensis,* and the one forb *Erigeron ramosus.*

Seedlings of 22 species of grasses appeared during the 4 years. They included *Andropogon furcatus,* 10 plants; *A. scoparius,* 1; *Aristida oligantha,* 2; species of Bouteloua, 6; *Elymus canadensis,* 13; *Festuca octoflora,* 344; *Koeleria cristata,* 613; Muhlenbergia sp., 7; *Panicum scribnerianum,* 67; *Poa pratensis,* 4,437; *Sorghastrum nutans,* 1; and *Stipa spartea,* 1. A considerable number of weedy grasses germinated. Of these only *Bromus tectorum* produced a large number of seedlings (259). Twelve seedlings of sedges and over 20 of rushes were found.

Fifty-one species of forbs were represented. The largest number, 29 species, germinated in sod obtained in the fall of 1930. Annuals included *Androsace occidentalis* Pursh, 5 specimens; *Hedeoma hispida* Pursh, 6; *Linum sulcatum* Riddell, 13; *Polygala verticillata* L., 7; *Silene antirrhina* L., 45; and *Specularia perfoliata* (L.) A. DC., 10. Typical perennials in-

cluded *Anemone cylindrica,* Nutt., seedling; *Astragalus crassicarpus* Nutt. (*Geoprumnon crassicarpum* (Nutt.) Rydb.), 3; *Comandra umbellata* (L.) Nutt., 3; *Erigeron ramosus,* 352; *Fragaria virginiana* Duchesne, 1; *Galium aparine* L., 2; *Helianthus rigidus,* 3; *Kuhnia glutinosa,* 2; species of Lithospermum, 3; Meibomia sp., 1; *Oenothera biennis,* 1; *Oxalis stricta* L., 110; species of Petalostemon, 10; Physalis sp., 1; species of Psoralea, 24; species of Solidago, 5; *Steironema ciliatum* (L.) Raf., 3; *Verbena stricta,* 2; *Vernonia baldwini,* 8; and *Viola pedatifida* G. Don, 9. From 10 to 15 species belonged to the group of ruderals; *e.g.,* *Ambrosia artemisiaefolia* L., 1 seedling; species of Brassica, 2; *Bursa bursa-pastoris* Brit., 3; *Chenopodium album* L., 3; species of Lactuca, 5; species of Lepidium, 48; *Leptilon canadensis* (L.) Brit., 12; *Rumex altissimus* Wood, 2; species of Sisymbrium, 6; and *Taraxacum taraxacum* Karst., 3.

DISCUSSION

In contrasting the germinations in frozen and unfrozen sod, it was impossible to determine whether the failure of a species to appear in one of the duplicates was due to exposure or protection in the matter of freezing or to the absence of seeds. Few species were represented by sufficient numbers to be dependable indicators of the effect of freezing.

A few examples of apparent benefit from freezing may be cited. The total number of Festuca seedlings was 245 from the frozen sod and 99 from that which had not been frozen. *Panicum scribnerianum* and *Oxalis stricta* consistently gave more germination in frozen than in unfrozen sod. For the former the respective yields were 52 and 15; for the latter, 89 and 21. *Andropogon furcatus* produced 10 seedlings during the 4 years. Nine were from sod which had been frozen. This was in agreement with the higher percentage of germination of seeds which had been frozen in dry storage, compared to the unfrozen seeds of the species, in the regular winter tests.

The reverse effect is suggested by the record of Koeleria. Each year the unfrozen sod had more seedlings than the frozen duplicate, with totals of 453 and 160 respectively. Germination tests, on a percentage basis, indicated slightly better germination from frozen seeds. *Poa pratensis* showed the same tendency. With the exception of one year, the seedlings were more abundant in unfrozen sod (3,614) than in frozen sod (823). Over 3,000 of the unfrozen seeds germinated in the sod of 1930. The largest number of seedlings of both these prolific species appeared in November. Tests of frozen and unfrozen seeds did not support this result. Probably it was due to the presence of large numbers of seeds of poor quality. Such seeds were able to germinate for a few weeks. They lost their vitality before the frozen sod was exposed to conditions conducive to development. *Erigeron ramosus,* with the exception of one year, produced somewhat more seedlings in unfrozen than in frozen sod, 188 as against 164. The observation of many

seedlings of Erigeron was made in the prairie each fall before frost. It was not certain whether they came from the unfrozen seeds which had fallen during the summer, or were developed from seeds which had lain in the ground through the previous winter. Of 5 specimens of Androsace found in two years, all except one were from unfrozen sod.

Seedlings of typical prairie species germinate in greater numbers under greenhouse care than under natural conditions. Large areas of prairie must be searched to yield the variety and number of individuals found in the surface area employed in the experiment. Absence of favorable combinations of heat and moisture, or sudden drying of a seed when germination has progressed to a critical stage are the chief causes of death of viable seeds before they can produce seedlings. Destruction by animals also is greater out-of-doors.

CONCLUSION

Relatively few of the viable seeds which fall on the prairie germinate under natural conditions.

GERMINATION IN THE PRAIRIE

Search was made for seedlings in the spring of the 4 years of 1929 to 1932. Similar observations were made in the fall in 1929 and 1931. The results of this study are qualitative rather than quantitative, as relatively large areas had to be inspected in order to obtain a variety of species or an appreciable number of those which were more abundant.

METHODS

Quadrats 35 centimeters square were located at random over considerable areas of prairie. Any seedlings present were listed. Unless they were to be studied later, young plants without cotyledons were excavated to make certain that the shoot had not arisen from an old plant.

DISCUSSION

Immediately after warm rains, as during the charting of some quadrats in July, 1929, the numbers of seedlings found were much larger than usual. Subsequent investigation showed that such germination amounted to very little, if any, permanent establishment. Only by germination in spring or fall do seedlings ordinarily have a chance to escape destruction by summer drought. After the first summer's observation, search for seedlings was not made after the middle of June or before the middle of October.

Most of the species which occurred in significant numbers were found in both spring and fall. *Meibomia illinoensis,* however, represented by a total of 17 seedlings during 4 years, was seen only in the spring and was found during each spring of the study. *Kuhnia glutinosa, Liatris punctata,* and Helianthus sp. were found exclusively in the spring, and occurred in very

small numbers during only two years of the four. Accordingly, the results from the observations of the 2 seasons have not been considered separately, but have been grouped by years.

RESULTS

Relatively few seedlings were found, although during the 4 years 42 species of forbs and 6 of grasses were observed. For any single season the number was small. Six species of forbs were seen each year: *Erigeron ramosus, Lactuca ludoviciana* (Nutt.) DC., *Meibomia illinoensis, Oxalis stricta, Senecio plattensis* Nutt., and at least one species of Solidago. Four other species seen during 3 years were Lepidium sp., *Linum sulcatum, Melilotus alba* Desv., and Petalostemon sp. The list of forbs recorded during 2 years included *Achillea occidentalis, Amorpha canescens, Anemone cylindrica, Aster multiflorus,* Carduus sp., Helianthus sp., *Kuhnia glutinosa, Liatris punctata, Lithospermum arvense,* Physalis sp., *Psoralea floribunda, Specularia perfoliata,* and species of Viola. Seedlings of two shrubs, *Rhus toxicodendron* L. (*Toxicodenedron rydbergii* (Small) Greene), and *Rosa arkansana* were also seen during 2 years.

Very few kinds of grass seedlings were observed. Of a total of 6 species, only *Panicum scribnerianum* was found each year. *Festuca octoflora, Koeleria cristata, Panicum capillare,* and *Poa pratensis* were all present during two years. A species of Andropogon was observed once.

During 1929 a total of 583 seedling forbs was found, comprising 22 species. Four of them were ruderals. Of typical prairie plants, *Erigeron ramosus* furnished 391 seedlings; *Achillea occidentalis,* 38; *Senecio plattensis,* 25; *Oxalis stricta,* 22; *Aster multiflorus,* 17; *Meibomia illinoensis,* 8; *Anemone cylindrica,* 6; *Antennaria campestris, Artemisia gnaphalodes,* and *Echinacea pallida,* 5 each; Solidago sp., 4; and other species even smaller numbers. Among the grasses *Koeleria cristata* was represented by 133 seedlings; *Festuca octoflora* by nearly a hundred; *Panicum scribnerianum* by 7; and *P. capillare* by 3.

In 1930 only 8 species of forbs were recorded. *Erigeron ramosus* again furnished the largest proportion, 8 plants of the total list of 17. Solidago sp. and *Specularia perfoliata* were represented by 2 seedlings, other species by only one. Eighty seedlings of *Koeleria cristata* and 34 of *Panicum scribnerianum* composed the grasses.

In 1931 thirty species and 249 individuals comprised the forbs. *Erigeron ramosus* again headed the list with 51 plants. If the ruderals are disregarded, the more abundant representatives are *Oxalis stricta,* with 45 seedlings; *Psoralea floribunda,* 23; *Salvia pitcheri,* 18; *Lithospermum arvense,* 16; *Linum sulcatum,* 13; *Oenothera biennis,* 6; Physalis sp., 8; *Senecio plattensis,* 6; 5 each of *Baptisia bracteata* A. Gray and *Meibomia illinoensis;* 4 each of *Hedeoma hispida* and Viola sp.; and 3 each of *Amorpha canescens,*

Helianthus sp. and also of the shrub *Rhus toxicodendron*. The list of grasses included 5 species and 46 seedlings. These were *Poa pratensis,* 20 plants; *Panicum scribnerianum,* 10; *P. capillare,* 8; *Festuca octoflora,* 7; and one of a species of Andropogon.

In 1932 twenty-two species of forbs and 127 seedlings were found. They included *Erigeron ramosus,* 32 plants; *Specularia perfoliata,* 30; *Anemone cylindrica,* 7; *Psoralea floribunda,* 6; *Vernonia baldwini,* 5; 3 each of *Lithospermum arvense* and *Meibomia illinoensis;* and 2 each of *Amorpha canescens, Liatris punctata, Oxalis stricta,* Petalostemon sp., *Scutellaria parvula* Michx., *Senecio plattensis,* and Solidago sp. Four seedlings of *Panicum scribnerianum* and 3 of *Poa pratensis* composed the record of grasses.

Where subsequent investigation of seedlings was possible, establishment was much less common than destruction.

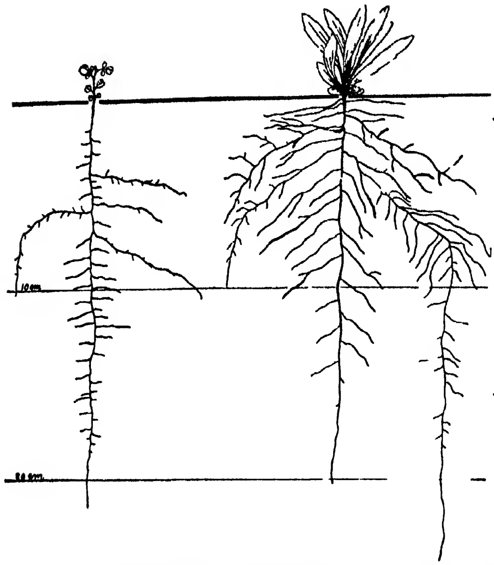
CONCLUSION

Except for the relatively few annual and short-lived plants, germination resulted in small numbers of widely scattered individuals, which frequently failed to survive.

EARLY LIFE HISTORY OF PRAIRIE PLANTS

After germination the seedling is under the immediate necessity of developing a root system and a foliage surface which will make it self-supporting when the supplies stored in the seed or cotyledons are consumed. The root grows rapidly and penetrates the deeper soil which remains permanently moist (Fig. 2). Unless it is able to accomplish this, the development of the entire plant will be slow. Low water content necessitates a considerable area of absorbing surface to furnish water at the rate demanded by the growing top. If drought overtakes the young plant, the shoot is unable to elongate and the leaves are small and lack turgidity. Photosynthesis, in the deepening shade of the established vegetation, becomes impossible. The result is death by starvation. Contact with the supplies of water in the deeper soils is effected promptly in the normal development of seedlings. This enables the seedling which germinated in the spring to live through the heat and occasional drought of summer. It assists the seedling which germinated in the fall to accumulate in its relatively limited tissues the reserve materials which maintain its diminished metabolism throughout the winter.

The rate of development has been studied in both controlled and natural environments. Two aspects of growth under optimum conditions have been considered. The development of roots in relation to tops was investigated in the greenhouse. The development of shoots of seedlings in a garden was followed throughout the growing season. To determine the early history in nature, seeds were planted in the prairie in the spring and the fate of the seedlings was observed throughout the summer. Seedlings which had germi-



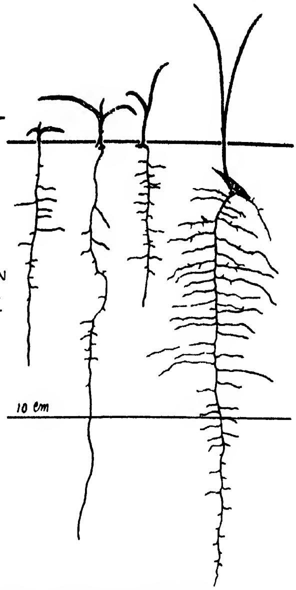
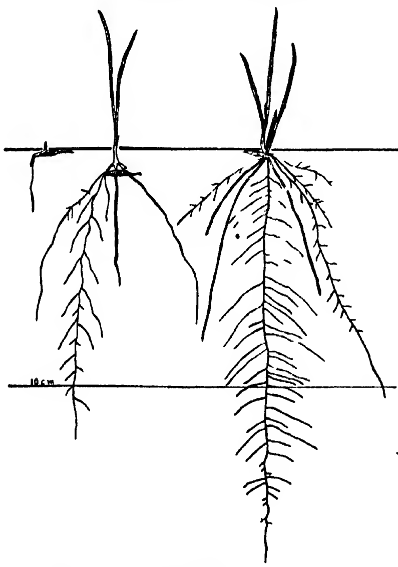


FIG. 3 Seedlings of *Amorpha canescens* (left) and *Solidago glaberrima*, about 6 weeks old

FIG. 4 Early development of grass seedlings two stages of *Panicum virgatum* (left); *Bouteloua curtipendula* (center), and *Stipa spartea* (right)



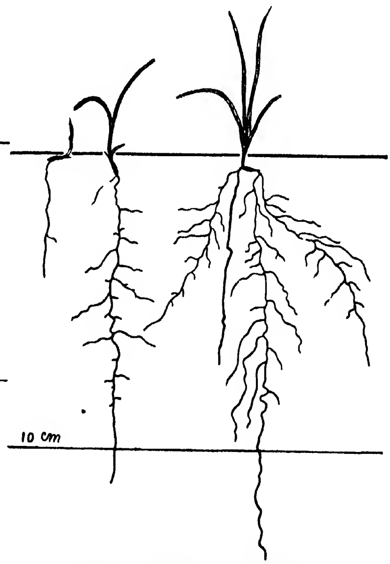


FIG. 5 Three stages in the development of *Elymus canadensis* seedlings one, thirteen, and seventeen days old

FIG. 6 Three stages in the development of *Andropogon furcatus* seedlings three, eleven, and twenty-two days old

nated naturally in the fall were located in late autumn and inspected again in early May.

DEVELOPMENT OF ROOTS IN RELATION TO TOPS

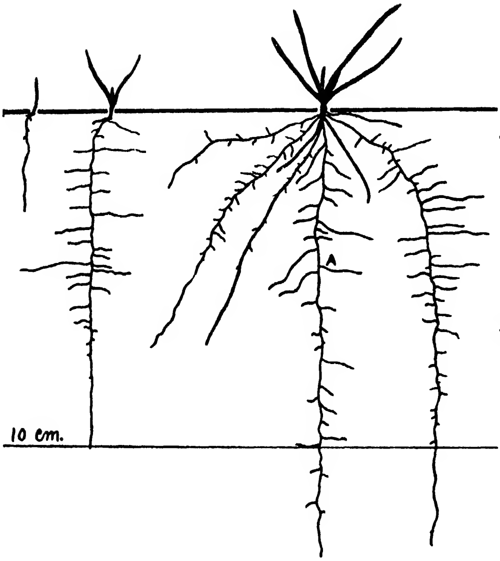
In soil uniformly supplied with water, oxygen, and nutrients, species show characteristic habits of growth. *Solidago glaberrima,* for example, possesses a diffuse root system with a wide lateral spread immediately below the soil surface but *Amorpha canescens* produces a strong taproot with short laterals growing out at right angles (Fig. 3). Only after study of control plants is it possible to evaluate the influence of environment. The root systems of young seedlings have been investigated for a considerable number of grasses and forbs.

METHODS

The seedlings were grown in a specially constructed series of wooden boxes. The depth of each box was 20 cm. and the surface area of the interior was 20 by 20 cm. One side was attached by means of brass screws, so that it could ' removed. The boxes were filled with soil of good tilth, firmed but not packed. This permitted growth to take place equally well in any direction through the soil. Watering was done sparingly.

RESULTS

Rapid increase in absorbing surface was illustrated by all of the grasses (Fig. 4). The root makes considerable elongation before the shoot appears above ground, sometimes even before it escapes from the seed coat. In *Elymus canadensis* the laterals of the seminal root form early and branch widely (Fig. 5). *Andropogon furcatus* is a much more mesic species, characterized at maturity by great depth of root penetration (Weaver, 1919). This feature is foreshadowed in the early elongation of its seminal roots and the unusually prompt development of a conspicuous secondary root which grows directly downward (Fig. 6). *Koeleria cristata*, a species of much more shallow root habit, shows more extensive branching close to the surface than either of the bluestems (Fig. 7). The secondary root system of many of the grasses, such as *Koeleria cristata, Bouteloua gracilis,* and *Stipa spartea,* begins to appear at the time of tillering or shortly before (Fig. 8). Subsequent tillers are accompanied or slightly preceded by other adventitious roots. This is illustrated by the densely branched system of *Sorghastrum nutans* and the deeply but more sparsely rooted *Panicum virgatum* (Fig. 9). Weaver, Kramer, and Reed (1924) reported similar findings in the case of winter wheat. Under favorable conditions, organs of vegetative propagation form very abundantly during the first year. A spring seedling of *Spartina michauxiana,* by late October, had developed 27 large rhizomes from 2 to 10 cm. in length (Fig. 10). Corresponding development in forbs was seen in a specimen of *Achillea occidentalis* of the same age.



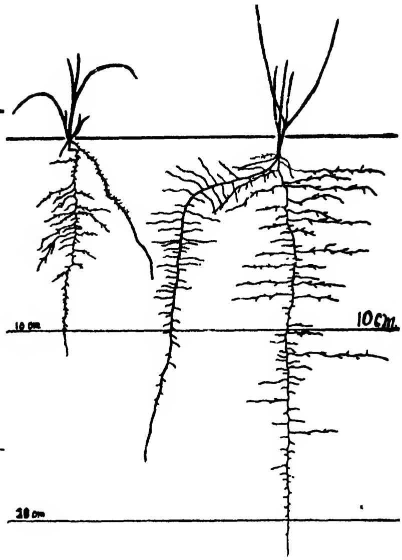
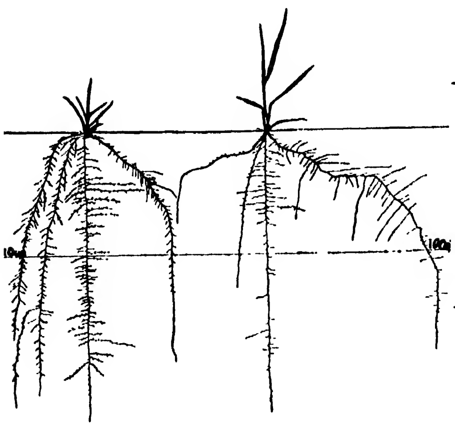


FIG. 7. *Koeleria cristata*, 4, 20, and 31 days after germination. The absorbing area afforded by the seminal root (A) has been greatly augmented by the development of several adventitious roots.

FIG. 8. Development of tillers and adventitious roots in *Bouteloua gracilis* (left); and *Stipa spartea*, between 4 and 5 weeks old.



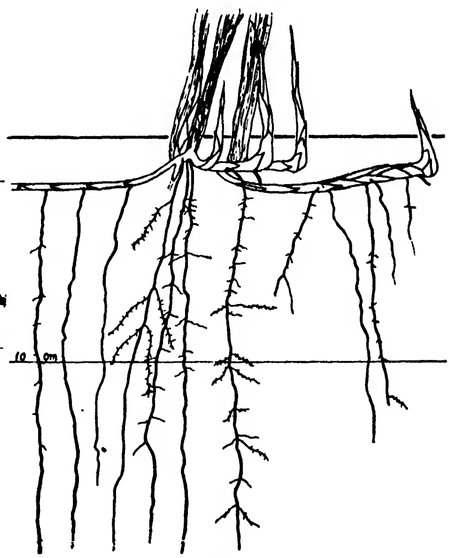


FIG. 9. Adventitious roots and tillers of *Sorghastrum nutans* (left) and *Panicum virgatum*, about 6 weeks old.

FIG. 10. Portion of *Spartina michauxiana* at the end of the first summer, showing abundant rhizomes and coarse roots.

Native dicotyledonous plants show the same rapid development of roots compared with tops, as is illustrated by *Oenothera biennis* (Fig. 11). An unbranched taproot is commonly extended to a depth of several centimeters while the cotyledons are unfolding. Such composites as *Liatris punctata* and *Kuhnia glutinosa* also demonstrate this phenomenon (Fig. 12). In Liatris, growth below ground is much more significant than expansion of the top during the entire first year. While a single narrow leaf represents the shoot for a long time, thickening of the taproot in the region immediately below the ground level becomes apparent very early. Even under partial shade and adequate water supply in a garden, development of the shoot was confined to a basal rosette but storage below the soil was pronounced in June. It resulted by late October in an enlargement nearly a centimeter in diameter. *Kuhnia glutinosa,* a species which is capable of fruiting during its first season, developed more leaf surface in comparison with the young root system. *Antennaria campestris,* a species of wide distribution in the prairie, is found most abundantly in areas of thin or sandy soil. As it is prevernal it is exposed for a long time to full sunlight. Like *Koeleria cristata* among the grasses, it branches widely in the upper soil (Fig. 13). The leaves remain small and few while the absorbing organs are prolonged as a taproot with extensive laterals.

CONCLUSIONS

Upon germination plants of the prairie rapidly developed a deeply penetrating root which often has lateral branches before much of the shoot is exposed to water loss. In the grasses tillering begins at the same time as the development of the secondary root system. Both grasses and forbs frequently develop rhizomes or other off-shoots after only a few weeks of growth, while continuing their root formation with equal rapidity. During all stages of development, growth of foliage is relatively slow and small compared to that of underground parts.

SHOOT DEVELOPMENT OF SEEDLINGS IN A GARDEN

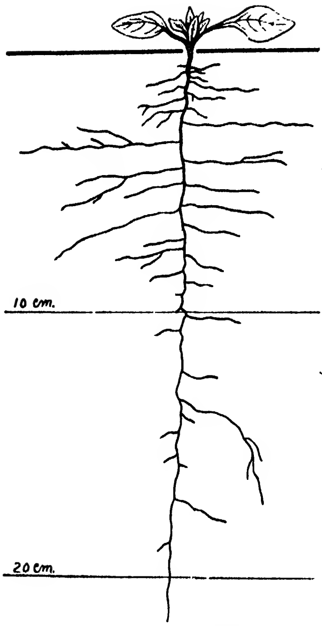
Several species of perennial grasses and forbs were grown in a garden to determine their development under favorable conditions during a single summer.

METHODS

The seeds were planted in pots in the greenhouse about the middle of April. The seedlings were transplanted to the garden on May 15. The soil was well watered and kept free from weeds until the middle of August. For a time the seedlings were protected from direct sunlight for several hours each day. The crop of seeds obtained was tested for germination.

RESULTS

Of 14 species of grasses, 9 produced viable seed the first year. They were *Andropogon furcatus, Aristida oligantha, Bouteloua curtipendula, B.*



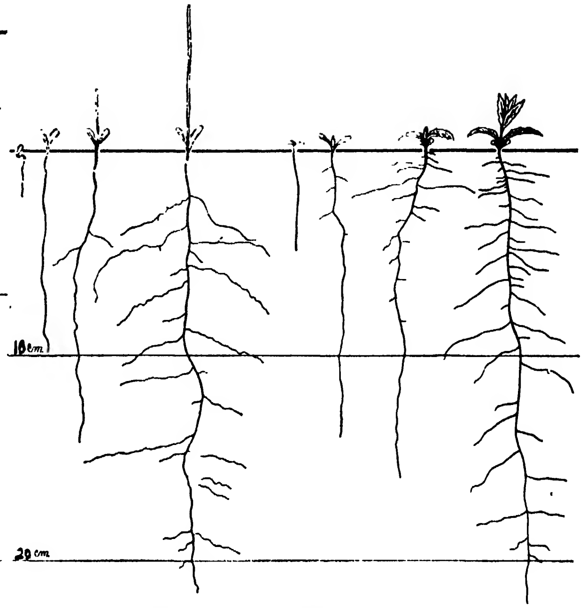
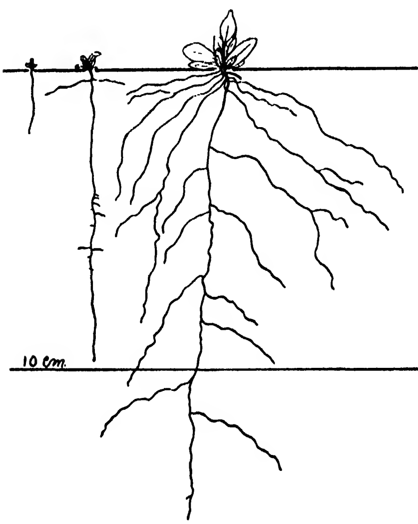


FIG. 11. Seedlings of *Oenothera biennis* showing single pair of leaves unfolded and taproot.

FIG. 12. Seedlings of *Liatris punctata* (left) 1, 4, 8, and 16 days after their appearance above ground, and seedlings of *Kuhnia glutinosa* of similar ages.



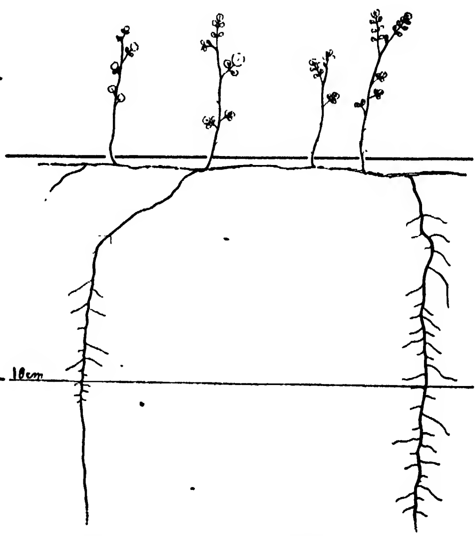


FIG. 13. Stages in the growth of *Antennaria campestris* showing the early development of an extensive surface absorbing system. The plants are 12, 24, and 56 days old, respectively.

FIG. 14. *Amorpha canescens* in early June, showing vegetative propagation from rhizomes.

gracilis, B. hirsuta, Panicum virgatum, Sorghastrum nutans, Spartina michauxiana, and *Sporobolus asper.* The seeds of 3 species gave remarkably high germination: *Andropogon furcatus,* 23 per cent; *Aristida oligantha,* 75 per cent; and *Bouteloua curtipendula,* 30 per cent. The germination from *Bouteloua hirsuta* was less than one per cent. *Elymus canadensis* formed heads which appeared normal but no seeds were present. Good vegetative growth but no flower stalks were obtained from *Agropyron smithii* and *Stipa spartea. Andropogon scoparius* failed to become established after being transplanted.

Of 21 perennial forbs, only 6 were induced to bloom during the first year and viable seeds were produced by only 3, *viz., Kuhnia glutinosa, Physalis lanceolata,* and *Vernonia baldwini. Oenothera biennis* fruited freely but no germination was obtained from its seeds. *Achillea occidentalis* flowered in October, too late to form seed. *Salvia pitcheri* blossomed abundantly but the branches were accidentally broken before the seeds ripened. In all of these species the stature of normal, mature plants was attained.

Antennaria campestris and *Astragalus canadensis* died early in the summer from lack of sufficient protection from the sun. *Aster multiflorus* formed only a basal rosette. *Amorpha canescens* and Petalostemon sp. were continually injured (possibly by rabbits) and did not reach 10 cm. in height. *Lespedeza capitata* grew to 15 cm. and was decapitated in August. *Liatris punctata* and *L. scariosa* formed only basal rosettes, but excellent storage organs. Clements and Weaver (1924) have brought these species to fruit in one season. *Solidago rigida, Silphium integrifolium,* and *S. perfoliatum* L. produced large basal rosettes. In the second spring the two rosin-weeds resumed growth early and suffered little harm from subsequent freezing weather. They fruited heavily in the summer. The ruderal *Tragopogon pratensis* made only foliage growth.

CONCLUSIONS

Many of the long-lived prairie species, which do not bloom ordinarily until their second or third year are capable, under favorable conditions, of forming normal amounts of foliage and viable seed during the first year.

SEEDLINGS IN THE PRAIRIE

In tracing the history of seedlings of perennials, the first difficulty is to make certain that the young shoots arise from seeds rather than from underground parts of established plants. Unless cotyledons or seed coats are found, the proof, in most cases, depends upon following the root system until a clear demonstration is afforded that the plant originated from a seed of the current season. *Helianthus rigidus,* for example, initiates growth each spring with leaves which can scarcely be distinguished from those of seedlings. The majority of apparent seedlings arise by vegetative propagation

from older plants (Fig. 14). Further, the seedlings found growing in the prairie are nearly always so few and so widely scattered that they do not form an adequate basis for recording the development of most species (Steiger, 1930). In order to obviate these difficulties in studying the establishment of native seedlings, seeds were planted in undisturbed prairie.

Growth begins to be generally apparent on the prairie early in April. It consists almost entirely of new shoots from established vegetation and normally seedlings do not appear in abundance until 3 to 4 weeks later.

The seeding was done at Belmont prairie, directly north of Lincoln, early in April of two consecutive years, 1930 and 1931. Plantings were made in two types of prairie: upland, along the top of a small ridge; and lowland, the nearly level ground at the foot, at a distance of about 50 feet from the upland station. *Andropogon scoparius* dominated the upland but there was also a considerable mixture of *Koeleria cristata* and some *Andropogon furcatus.* The grass of the lowland was an almost pure stand of *Andropogon furcatus.*

METHODS

Two types of seeding were used, surface sowing and shallow planting. For surface sowing, the soil was loosened with the blade of a small knife. The seeds were sprinkled into the debris and slightly mixed with it, to prevent blowing and to simulate the effect of planting by nature in autumn. For shallow planting, the ground was broken and the seeds were placed in it and covered to a depth of one-fourth to one-half inch, depending upon their size.

On both upland and lowland two lines of planting were made, one of seeds sowed on the surface and one of shallowly planted seeds. A small stake at the place of planting of each species made it possible to relocate the seedlings.

The seeds were from the harvest of the preceding fall. They had been stored dry and frozen out-of-doors during the winter. Approximately equal, measured quantities of seeds of each species were used for each planting at both stations. The unit was somewhat over 100 seeds except when high germination could be expected; then the number was reduced to about 50.

The seeds were planted early in April. Examination for germination and development was made at intervals of about one week until the middle of May, and on alternate weeks after that time. Inspection was discontinued only after the advent of killing frost. Search for winter survival was conducted during the following spring.

Soil moisture was determined at depths of 0 to 6 and 6 to 12 inches during very dry periods in July, when conspicuous numbers of seedlings were dying. Light intensity among the seedlings was determined at inter-

vals. Access was also had to hygrothermograph, anemometer, and atmometer records at a station of a co-worker only a few rods distant.

SPECIES TESTED

Seventeen species of grasses were tested during the two years. Fourteen of these were planted both years. They included the prairie dominants, *Andropogon furcatus, A. scoparius, Bouteloua curtipendula, Elymus canadensis, Koeleria cristata, Panicum virgatum, Sorghastrum nutans, Sporobolus heterolepis* A. Gray, *Stipa spartea,* and *Sporobolus asper.* Two typical, low-growing grama grasses, *Bouteloua gracilis* and *B. hirsuta,* were planted both years, and the preclimax *Aristida oligantha,* which usually occurs along the edge of the prairie as a ruderal. *Bulbilis dactyloides* and the ruderal grasses, *Chaetochloa glauca* and *Panicum capillare,* were tested during one year only. *Carex festucacea* Schkuhr. was planted each year.

Thirty species of forbs were planted, 22 of them during both years. They included *Achillea occidentalis, Amorpha canescens, Antennaria campestris, Artemisia gnaphalodes, Aster multiflorus, A. salicifolius, Astragalus canadensis, A. crassicarpus, Echinacea pallida, Gaura parviflora* Dougl., *Glycyrrhiza lepidota, Helianthus rigidus, Kuhnia glutinosa, Lespedeza capitata, Liatris punctata, L. scariosa, Meibomia illinoensis, Oenothera biennis,* species of Petalostemon, *Physalis lanceolata, Salvia pitcheri, Silphium integrifolium, S. laciniatum* L., *Solidago canadensis* L., *S. rigida, Verbena stricta,* and *Vernonia baldwini. Grindelia squarrosa,* often seen in this region in overgrazed prairie, and the ruderals, *Helianthus annuus* and *Tragopogon pratensis,* were also planted.

CONDITIONS FOR GROWTH

Cool weather marked the beginning of the growing season of 1930. The soil was well supplied with water and the air was quite humid during the spring and early summer. From the middle of June until the second week of August, extreme heat and drought characterized the season. Considerable rain fell in the last half of August. September was warm and dry. In 1931 the spring was relatively dry.

The rain of both May and June fell in brief, heavy showers. June was very hot. The most sustained season of drought occurred during the first half of September.

The seeds planted in 1930 were from a harvest which yielded a much higher percentage of germination than the seeds planted in 1931. The latter were collected after the exceptionally hot, dry summer of 1930. The germination in the field in 1930 was somewhat higher than that of 1931 in respect to number of species, and considerably higher in number of individuals. In 1931 the lowland seedlings suffered a casualty which was not normal to the prairie. They were situated where, under unusually heavy precipitation,

they received the wash from a cultivated field. Torrential showers late in May resulted in the burial of the seedlings of more than 50 per cent of the species which had germinated.

RESULTS

Differences from the two types of seeding were less apparent in the greater soil moisture during the spring of 1930 than during the following year. More seedlings were produced at both upland and lowland stations from planted seeds than from surface sowing. The differences, however, were seldom large. Sometimes a species, at one station or the other, gave a higher germination from surface sowing. On the whole, however, pushing up through the soil was less of a handicap than contact with the drier air above ground. No appreciable difference in time of appearance was detected. Since inspection was made at intervals of one to two weeks, the actual dates of germination were somewhat earlier than the recorded dates and small differences in time of germination were not seen. After the seedlings appeared above ground, their growth was not affected by the type of planting. The plants obtained from both methods of sowing have, accordingly, been considered as forming one group for each species at both the upland and the lowland stations.

No permanent establishment was obtained during either year. A small number of species, represented by a few individuals, survived until late summer. Before the following spring, however, and sometimes before the frosts of autumn, these perished.

Some of the plantings, especially in the drier soil in the spring of 1931, produced so few seedlings that a study of the species had to be based on very small numbers of individuals. As isolated plants frequently attained better growth than seedlings closely grouped, the development of even one or two plants has been permitted to serve as a record for the species.

Eighty-eight per cent of the grasses planted in 1930 germinated; *i.e.*, 15 species of a total of 17. Fifty per cent of 16 species germinated in 1931. *Sorghastrum nutans* grew only at the upland station. *Bulbilis dactyloides* and *Sporobolus heterolepis*, each planted one year only, failed to give any germination. The other species were represented at both stations. There was always a possibility that a species germinated and perished before any record was obtained. As the study was made primarily to determine establishment, such an omission was not extremely important.

Three species were present on September 30 of the first year: *Elymus canadensis, Koeleria cristata*, and *Sporobolus asper* in the lowland and *Elymus canadensis* (germinated after the summer drought) in the upland. Each was represented by 3 or 4 plants, under 10 centimeters high, bearing less than 5 leaves. The following spring only Elymus in the lowland was present. The 3 little plants were buried later under debris. None of the seedlings

of 1931 survived through August. A sedge, *Carex festucacea*, failed to appear during either year.

Between 70 and 75 per cent of the 25 to 27 species of forbs germinated each year. The upland only produced seedlings of *Antennaria campestris, Aster salicifolius, Meibomia illinoensis, Oenothera biennis*, and *Verbena stricta*. *Astragalus crassicarpus* appeared only in the lowland. No germination was obtained from *Artemisia gnaphalodes, Aster multiflorus, Glycyrrhiza lepidota*, and the two species of Solidago. Germination was given by one Solidago a year after it had been sowed.

By September 30 of the first year 4 species were present: *Achillea occidentalis* in the lowland; *Amorpha canescens, Kuhnia glutinosa*, and *Lespedeza capitata* on the upland. The maximum height was 9 centimeters. None was found the following spring. The second year the last species to succumb were *Helianthus rigidus* on the upland and *Salvia pitcheri* at both stations. They attained a maximum height of 16 centimeters before they died in severe drought in September.

Seeds which germinated a year after being sowed included species of Amorpha, Astragalus, Echinacea, Lespedeza, Meibomia, Oenothera, Petalostemon, Salvia, Solidago, and Vernonia. Only Lespedeza survived until August. It was dead by November.

CAUSES OF DEATH

Several factors combined to produce this wholesale mortality of seedlings. Relatively long periods of drought are normal to the climate. They constituted the most conspicuous cause of death. While July was exceptionally hot in 1930 and June was unusually hot in 1931, the two summers were in general more typical of the growing season in Nebraska than years characterized by high rainfall. Destruction by insects and allied animals is a contributing cause to the disappearance of seedlings. Its toll of young plants is mainly exacted so soon after germination that many of them completely escape the notice of the observer. A fundamental factor in the failure of perennial seedlings to establish themselves in their native prairie is their slow growth.

Drought

For the seedlings which attained temporary establishment, the principal immediate cause of death was drought. Fifty-seven per cent of all the species which germinated at either station during the two years perished during the last 10 days of June or in July. The decrease in numbers of individuals during both years showed even more clearly the destructive effect of hot, dry weather.

Soil moisture determinations were made from samples taken with a Briggs geotome as close to the seedlings as possible without disturbing their water

supply. The available water content was calculated by deducting the hygroscopic coefficient from the total water content. In the surface foot on the upland during the first year the water content was below this point (7.5) by July 11. In the surface 6 inches during the second year it was within 2 per cent of the limit of availability by July 1. The water content of the lowland soil at the level of the roots of the seedlings was always somewhat above the hygroscopic coefficient (10).

While the established vegetation protected the seedlings from the direct rays of the sun and the low humidity of the air above the plant cover, it deprived them of water. Its mass of underground parts, extending to within an inch of the soil surface, possessed many fine roots which absorbed at the same level as the seedling. As conditions of drought developed mature vegetation, transpiring strongly, depleted the upper soil of its moisture and continued to exist by reason of its deeper root system. By midsummer the surface foot of upland soil was too dry to maintain the life of seedlings.

Animals

Insects and other arthropods caused injury and complete destruction to large numbers of newly germinated seedlings from the time of their appearance to the middle of June. With drier weather and older plants, their activities were less conspicuous.

The fluctuating count of seedlings obtained in the spring of 1930, during successive weeks of observation, indicated high losses. The probability of damping-off fungi was not great on the open prairie, nor were remains of plants rotted at the base seen on the ground. The finely bitten appearance of the leaf tips and the diminished numbers of plants in a group suggested the depredations of insects and allied animals. A few beetles of small to medium size and rarely the moulted skin of a millepede were observed near the seedlings. Young grasshoppers and small, ground-living beetles constituted the most probable source of injuries due to animals.

Grasses found with the tops bitten off included *Agropyron smithii* and *Sporobolus asper* on upland, and *Bouteloua curtipendula* and *Spartina michauxiana* in lowland. Many forbs suffered partial destruction of their leaves. Practically complete loss of the seedlings of some species occurred early in the season, after conspicuous ravages had been made on the leaves. Replacement sometimes followed through additional germinations. Marked inroads were made each spring on the blazing stars. Many individuals of *Liatris punctata* and *L. scariosa* were continually pruned of their first typical leaf and reduced to the cotyledon stage.

The number of seedlings found was undoubtedly less than the total germination. Arthropods were decisive in preventing the development of many individuals. Young plants were destroyed or so weakened that they were unable to endure excessive shade or drought later in the season.

Slow Growth Due to Shade

When the food reserves in the seed or cotyledons have been exhausted, growth comes frequently to an apparent standstill. The period of greatest leaf formation and elongation for the majority of seedlings was found to follow immediately after germination. It seldom occurred later than the first week of June. The check to vigorous growth usually came before the season of drought. The cause appeared to be the presence of established vegetation. The permanent grasses had become so tall that the seedlings were too deeply shaded to make much food.

Clements and Weaver (1924) found that seeds planted in denuded quadrats produced 4 times as much establishment in prairie at Lincoln as seeds which were so planted that the seedlings grew in the shade of mature vegetation. Surface sowing resulted in competition at all periods, beginning with germination and continuing with development of seedlings which were soon undergoing shortage of both water and light. They prepared quadrats by destroying all vegetation present, so that only seedlings used the factors available for growth. Although the water relations were poorer because of the breaking of the cover of vegetation, the increase in light more than compensated for the decrease in moisture.

Light intensity in late May, at the surface of upland prairie burned the previous spring, was found, in the same study, to range from 2.5 to 26 per cent. In our experimental area, among the seedlings in July light commonly varied from 3 to 15 per cent in the upland and 2 to 10 per cent in the lowland. Readings as high as 62 per cent were taken among the upland seedlings, but the plants were small and wilted as the result of excessive transpiration and dry soil.

The late start of seedlings in spring was primarily responsible for their limited growth. Low temperature was the first retarding influence. While it was adequate in April for shoot production from perennating parts of mature plants, it was too low for rapid germination and seedling development. The average soil temperature in April (from records taken at Lincoln for 12 years) in the upper 3 inches of soil is 56° to 58°F. In May the averages are 10° to 12° higher. While an abrupt decrease in water content commonly occurs in late May, the first 3 weeks of the month present the optimum combination of habitat conditions for germination. Much the largest number of seedlings appeared during that period.

Where a group of seedlings consisted of closely crowded individuals, all died sometimes before the general water supply became critical. Eight specimens of *Gaura parviflora* in 1930 formed a small, uniform mass. From their germinations (April 25 to May 9) to their disappearance, almost no growth could be detected. On June 6 the clump was hardly more than a centimeter high, 5 plants were dead and the others wilted beyond recovery.

Inability to get enough water and nutrients in a much restricted area had so stunted them that they were unable to endure the first drying of the surface soil. In such instances death was due to competition among the seedlings.

Crowding of seedlings often resulted in the prompt death of some, the maintenance of suppressed existence by most and the elongation of a few far beyond the general level; *e.g., Salvia pitcheri.* The dominants survived the rest of their group by several weeks. They appeared to be little harmed by the stand of low, weak plants which surrounded them for a considerable time. Their greater stature and longer period of life emphasized the advantages of rapid growth as a factor in establishment.

The majority of individuals died within the space of a single week, probably during a critical day or two of extremely hot, dry weather. Such periods of drought are characteristic of prairie climate. Only once in a considerable number of years do they fail to occur. Well rooted plants alone can withstand them. Seedling growth in prairie is uniformly too slow to escape destruction.

CONCLUSIONS

Germination is retarded by the low temperatures of April. Insects destroy considerable numbers of very young plants. Seedlings present little foliage until new shoots of established vegetation are sufficiently enlarged to reduce greatly the light near ground level. As a result they are unable to form adequate leaf surface for photosynthesis. Their roots are starved for carbohydrates and deprived of water by the more efficient absorbing systems of mature, rapidly transpiring plants. Incapable of growing up into the light or of extending into the subsoil for water, seedlings usually lead a suppressed existence and perish in the first drought of summer.

Sufficient establishment obviously occurs in nature to maintain the prairie. The dominant plants of dry regions are highly specialized (Bews, 1929). In a climate poorly suited to the development of seedlings, a type of vegetation has been evolved which requires relatively little replacement. Long life of the individual and much vegetative reproduction are characteristic of grasslands. A few seedlings may become permanent each year, mainly in disturbed areas. Most of the establishment, however, probably occurs in natural prairie during the rare growing seasons of excessive moisture.

SURVIVAL OF SEEDLINGS DURING WINTER

The amount of winterkilling of seedlings found growing in the prairie in the latter part of October was studied during two separate years, 1929-1930 and 1931-1932. Seedlings were much more abundant in the former season than in the latter.

METHODS

Seedlings were located in unbroken prairie during the last ten days of October. Each individual or group of individuals growing closely together

was recorded and marked by a stake bearing a number. The middle of the following May, the stakes were relocated and the condition of the seedlings was observed.

CLIMATIC CONDITIONS

In 1929 the temperature during October was average with a maximum of 80°F. The minimum, 30°, did not occur until October 23. As killing frost was delayed until the sixth of November, and precipitation during October was very high, conditions favored germination and development of seedlings. The winter was, on the whole, severe. Snow covered the ground, however, much of the time until unusually high temperatures developed in February. In March the temperature was normal. The precipitation during both of these months was very low. In the absence of sufficient heat to stimulate growth, low precipitation does not appear to be injurious to prairie plants. Once they are well established, their endurance of drought during dormancy is great. Both temperature and precipitation were high in April, so that conditions were favorable for an early resumption of growth.

In 1931 the temperature in October was high, with a maximum of 91°F. on the tenth of the month and a minimum of 35°, not attained until the 31st. The precipitation was low. Germination on the uplands was prevented until very late in the month. Killing frost was recorded on November 1. The average temperature for November, however, was high (43.8°) and the precipitation was high, so that young seedlings probably made some growth. The winter temperatures were high except during January. An unusual amount of snow fell and the ground was covered most of the time. After a very warm March, April was cold. The precipitation during both months was well below the average. The May temperatures were high, while the precipitation continued low. Conditions in general were unfavorable for vigorous resumption of growth.

SPECIES

Erigeron ramosus and *Senecio plattensis* were the only forbs which regularly occurred in the fall in abundance. The seedlings of Erigeron were much the more numerous, as they often developed in thick clusters of plants. Senecio was represented by scattered individuals. Two species of Anemone were commonly present, *A. cylindrica* and *A. caroliniana* Walt. In the dry, hot autumn of 1931 Lithospermum germinated conspicuously. Thick cotyledons and occasionally a narrow leaf were present early in November. While seedlings of *Koeleria cristata* were abundant in the fall of 1929, only a few were found in 1931.

RESULTS

In 1929-1930 the survival of grasses appeared to be 100 per cent. About 135 seedlings of *Koeleria cristata* were located in the fall, forming low, dense groups. The number of plants present in the clumps in the middle of

the following May was larger. Whether or not some had died and been replaced by new germination, which was still occurring, could not be determined. Of a total of 44 forbs recorded, 32 were present in the spring, and with few exceptions were in a healthy condition. The spring inspection revealed the 3 plants of *Anemone cylindrica*, 4 of the 5 of *Aster multiflorus*, 11 of the 12 of *Erigeron ramosus*, the one specimen of *Psoralea esculenta* Pursh and all 13 plants of *Senecio plattensis*. A seedling of *Linum sulcatum* died, and 9 young plants which were too small to be identified. The total forb survival was 73 per cent.

In the fall of 1931 only 13 seedling grasses were found. They had such attenuated, wilted leaves that identification was difficult. Several plants of *Festuca octoflora* survived. They were, however, so nearly dead that it was practically certain that they would perish during the first hot days. Three specimens of *Poa pratensis* and 3 others which were not identified had disappeared by the middle of May. The survival of grasses was 54 per cent. Forbs were represented by 45 individuals. *Anemone caroliniana*, *Galium aparine*, Lepidium sp., and *Senecio plattensis*, each with a record of 2 seedlings, survived, though specimens of Lepidium were diseased. *Erigeron ramosus* lost 1 of 5 seedlings; Lactuca sp., 2 of 3; *Linum sulcatum*, 1 of 7; and Lithospermum sp., 2 of 16. Of 6 seedlings too small to be identified, 5 perished and the other was too little developed to be recognizable. The total forb survival was 75 per cent.

DISCUSSION

By far the largest proportion of deaths occurred among the seedlings which were too small to be identified. Very few such specimens survived and grew until they could be recognized. Most of the plants of Erigeron were in the 6 to 8 leaf stage. Anemone and Senecio often appeared to have lost one or 2 leaves when located in the fall. Lithospermum had very large cotyledons. The grasses which failed to survive entered the winter greatly weakened by drought. During both seasons of study, snow covered the ground throughout the greater part of the winter months. The thick layer of dead grass, however, affords much protection to young seedlings. Even in the absence of snow, they are not exposed to the direct action of the wind or to the most sudden changes in the temperature of the air.

Corroboration of the success of grasses in surviving the winter, if they have had good conditions for growth in the fall, was afforded by two species in the garden. Twelve plants of *Stipa spartea* and 20 of *Elymus canadensis*, all seedlings from seeds which were planted as soon as harvested, lived through the winter. By late December the leaves of Stipa had died back to a height of 2 cm. Those of Elymus were green for 5 cm. and apparently suffered little injury during the winter. Both species resumed active growth early in

spring. The winter survival of certain economic species which were seeded in the fall has been treated by Keim and Beadle (1927).

CONCLUSION

Vigorous fall seedlings of forbs which have developed to the third- or fourth-leaf stage or of grasses which have attained the second- or third-leaf stage show a survival through the winter of 80 to 100 per cent.

SUMMARY

Seeds of 42 species of plants of tall-grass prairie were tested for germination by plantings made in soil. The percentage of germination was ascertained and also the length of time after planting before the largest proportion of seedlings appeared.

The seeds were gathered when ripe from plants growing naturally in undisturbed prairie. A résumé is given of the environmental conditions under which they developed and to which germinating seeds and seedlings were subjected in nature.

Seeds of 10 species, planted 6 to 7 times during one year and in 8 successive months after another harvest, showed wide fluctuations in germinative power. It was, as a rule, very low at harvest time, highest in spring, often nearly as high early in the following autumn, but low in winter and midsummer. Frequently monthly variations were so great as to obscure the real viability, when germination was made the criterion. Hence, tests of germination should be made at the time of year most favorable to the development of the seeds. This is usually April and May.

Viability of seeds kept in dry storage at room temperatures was tested for 7 species of grasses and 4 of forbs. All except 2 grasses and 1 forb showed an almost complete loss of viability by the end of 5.5 years.

The seeds of 4 harvests were tested for 13 grasses and 18 forbs; those of 3 harvests for 2 other grasses and 9 other forbs. Several additional herbs were tested during 1 or 2 seasons. The percentage of germination varied considerably for any species from year to year and often from season to season. Germination of the seeds of most of the important grasses, when planted at a favorable time of year, ranged between 10 and 20 per cent; a few yielded over 40 per cent. The germination of the seeds of most forbs kept in dry storage was below 15 per cent, although in some species it was regularly at least 50 per cent.

The relative germination of seeds stored under different conditions was determined. Mature, air-dried seeds were stored out-of-doors but protected from precipitation and subjected to the freezing temperatures of winter. Similar seeds were stored indoors at living-room temperatures which were seldom below 50°F. In late winter, plantings from both lots were made in the greenhouse. Variability was observed from year to year in the state of

dormancy of the seeds at this season. For most species dormancy was broken for a larger proportion of the seeds which had been exposed to low temperatures. In addition many species were tested at other seasons. The time when a test was made was important for species in which it was difficult to break dormancy. Once the seeds were thoroughly ripened, a few species seemed to be almost as dependable as cultivated crops.

Stratification of seeds through the winter months resulted in marked improvement for many forbs and a few grasses. It produced the largest amount of increase in the germination of seeds of species which gave very low germination after dry storage either regularly or as the result of a poor growing season.

Most prairie species produced large numbers of seeds. Small but by no means negligible percentages of these were viable. The number of seedlings obtained varied greatly with the growing season preceding the harvest. Species producing seeds which gave germination of 50 to 80 per cent when grown in a relatively cool, moist summer were greatly handicapped in seed formation during seasons characterized by periods of drought. After such summers the same species sometimes produced seeds which gave a germination of less than 10 per cent.

The seeds of most prairie plants are subject to deep dormancy during the greater part of the year. Under conditions conducive to germination at seasons which are unfavorable for development they remain latent, no doubt with somewhat lowered vitality. Many develop subsequently if conditions again become suitable during the season which is normal to them for germination. The length of the latent period varied greatly with the season of planting. If this was favorable, most grass seeds germinated within 2 weeks and most forbs within 2 to 4 weeks. A few species of both grasses and forbs seldom produced many seedlings until the second month after planting.

Germination in the prairie was observed in spring and fall. There was relatively little as to both number of species and number of individuals. Comparatively few of the viable seeds which fell on the prairie germinated. Conditions were seldom favorable for a sufficient length of time for development of seedlings. Except for the few annual and short-lived plants, germination consisted of small numbers of widely scattered individuals which frequently failed to survive. Prairie sod brought into the greenhouse yielded relatively abundant germination in respect to both species and individuals.

Optimum water content for germination was found to be one-third to one-half saturation for seeds of species characteristic of uplands and one-half to two-thirds saturation for those of species of lowlands. Alternately high and low water content, with the resulting improvement in aeration, was satisfactory for seeds which germinated quickly.

The early life history of prairie plants has been studied in both controlled

and natural environments. A deeply penetrating root was developed rapidly, often with lateral branches before much of the shoot was exposed to water loss. This was a major adjustment to the prairie environment. Tillering in grasses began at the same time as the growth of the secondary root system. Organs for propagation and the accumulation of reserves of food were often developed very early.

Many of the long-lived species which do not set seed ordinarily until their second or third summer were found capable, under favorable conditions, of producing viable seed during the first year.

Establishment in the prairie sod was studied by measuring the development of seedlings from seeds planted in the spring. Because of heat and drought, no establishment was obtained from two years of planting. Although a few seedlings remained at the end of one summer, they winter-killed.

The survival of seedlings which had developed in autumn from seeds scattered by the wind was determined in the middle of the following spring. Vigorous seedlings which had attained the third- or fourth-leaf stage showed, during each of two successive seasons, a winter survival of 80 to 100 per cent.

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AN ECOLOGICAL STUDY OF THE FRESH-WATER SPONGES OF NORTHEASTERN WISCONSIN*

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* From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey and the Thornton Junior College. Report No. 61.

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AN ECOLOGICAL STUDY OF THE FRESH-WATER SPONGES OF NORTHEASTERN WISCONSIN

HISTORICAL STATEMENT

Although fresh-water sponges have been the object of attention of students of freshwater biology for over half a century, and although the sporadic and erratic occurrence of sponges has been remarked by numerous workers, it is only recently that any definite attempts have been made to correlate sponge distribution with known environmental factors. One difficulty encountered by earlier workers has been the tendency to speak of "sponge distribution" as a single problem without specifying what species of sponge is under consideration. One would not attempt to discuss "bird habitats" without differentiating between woodpeckers and ostriches. It is not unlikely that as great a difference exists between the optimum habitats of two such sponges as *Ephydatia mülleri* (Lieberkühn) and *Ephydatia everetti* (Mills).

Potts (1887), records sponges from polluted waters "unfit for domestic use", but states their preference for pure waters. As to current he says "in my experience the finest specimens have always been found where they were subject to the most rapid currents. The lower side of large loose stones at the 'riffs', the rocks and foaming waters at the foot of a mill-dam fall, the timbers of a sluice-way, the casings of a turbine water wheel, or the walls of a 'tail race' beneath an old mill;—in all these places they have been found in great abundance and of very lusty growth." Shallow waters having a mud bottom are regarded as almost hopeless situations for sponges, whereas in water liable to be charged with heavy sedimentary material sponges may be sought on the lower sides of their bases of support or on perpendicular surfaces.

Modern limnological methods with their exact quantitative determinations were unknown in 1887. The paper by Potts is, nevertheless, a valuable contribution to the ecology of freshwater sponges for, under the discussion of each species which he collected himself, a description of a typical habitat is given. These descriptions, the work of an alert observer, are so vivid and accurate that the modern ecologist can all but check them against his chemically analyzed environment.

Stephens (1920) lists *Heteromyenia ryderi* Potts as a light-shunning form, and *H. repens* Potts, *Spongilla lacustris* (Linnaeus), and *Ephydatia fluviatilis* (auctorum), as limited by high calcium content. In her experience in Ireland she finds the most favorable sponge habitats to be rivers which drain lakes.

Smith (1921b) working in Michigan states, "There is abundant evidence that many favorable conditions for an abundant sponge fauna are present

in small bodies of water where there is not much wave action and where there is little or no silt. Enough current for circulation and renewal of the food supply is desirable, but only a few species thrive where the current is strong. Sloughs and channels which connect lakes are often favorable habitats."

Old (1932b), like Smith, fails to find the most sponges in the swiftest water and, contrary to the experience of Potts, records sponge colonies from the mud bottoms of ponds and from small sluggish streams. It is probable the "mud" from which Old collected sponges was largely organic detritus, whereas the "mud" found by Potts to be inimical to sponges was largely silt.

The author's interest in the *Spongillidae* was first aroused by Professor Frank Smith during her graduate work at the University of Illinois. Subsequently (in 1921) she again had the privilege of contact with Professor Smith at the University of Michigan Biological Station, and of accompanying him on several collecting trips. During such excursions conversation frequently turned to the variety of ecological problems furnished by sponge distribution, and unpublished observations, illustrative of the problems yet to be solved, were freely recounted by the elder scientist. He had found entirely different sponge faunas in two contiguous bodies of water. Sponges might be very numerous in one location while, in an apparently suitable location only a short distance away, not a specimen would be found. In one small bog, (Smith's Bog), which he had frequently visited, he had found a different sponge fauna at almost every visit; and the species most abundant at one time might be entirely lacking at a later date the same season, or at the same time the following season. While expressing the opinion that minute differences in the water, which a trained limnologist could detect, might account for these phenomena, he still refused to guess as to what these differences might be. When, in the summer of 1923, the author observed that Smith's Bog was not only subject to great variations in fauna, but that the quality of the water also underwent rapid fluctuations, changing from pH 4.3 to pH 6.8 within a period of three weeks, she promptly communicated this information to Professor Smith with the suggestion that, therein, might lie the solution to the sponge riddle. His reply was characteristic and generous, "I have enough Oligochaetes to keep me busy for some time, so am going to leave it to you to find out why sponges are distributed as they are; and shall be interested to know what you find out." While the author does not presume to interpret this remark as a "Cloak of Elijah", still this stimulating challenge may be regarded as remotely a cause of the present investigation.

Although this investigation was not begun until the spring of 1931, the desire to follow what appeared to be a good lead had smouldered for eight

years. It was, therefore, with great enthusiasm, that an invitation was received from Professor Juday to make use of the facilities of the Wisconsin Biological Survey while pursuing a study on the sponges of northeastern Wisconsin. Grateful acknowledgment is also made to Drs. Owen Nolf and Edward Schneberger for assistance in microphotography, and to the following students and members of the survey staff for cooperation in bringing in specimens and for assistance in handling boats and heavy apparatus; Dr. Edward Schneberger, Emerson McVey, Richard Wilson, Howard Field, and Hugo Baum.

It is doubtful whether any place in the world could be found better adapted to a study of the ecology of the *Spongillidae* than the Wisconsin State Biological Survey headquarters on Trout Lake. In Vilas County alone there are approximately eight hundred lakes and ponds, most of which have been mapped and are readily accessible. As a result of the extensive investigations of Drs. Birge and Juday with their corps of able assistants, one or more complete physical and chemical analyses has now been made of the waters of each of the larger and many of the smaller lakes. All of these data, unpublished as well as published, were most generously placed at the author's disposal; hence, to Drs. Juday and Birge, belongs the credit for the limnological data used in the following pages.

METHODS

In the smaller streams the sponges were collected by wading. In larger streams and lakes the collections were made from a boat. A garden rake was often used to bring submerged objects which might bear sponges within reach. The boats used for most of the collecting were a light 12 ft. duck boat and a pneumatic rubber boat. Sponges from depths of two or more meters collected from Crystal and Weber lakes were brought up by a Petersen dredge. Due to the weight of this apparatus it could not be used from either of the small portable boats. At the time of collection any characteristics of structure or growth form were recorded and the specimens were laid in wire screen trays to dry. When dry, a part of each sponge was mounted for identification and the remainder of the specimen placed in an envelope bearing the name, location, and date of collection.

Slides for rapid identification were prepared by boiling a fragment of the sponge on the slide in three or four drops of concentrated HNO_3, washing in alcohol, then xylol, and mounting in balsam. When better preparations were desired for more detailed study or microphotography, a fragment of the sponge was placed in a test tube with 10 to 15 cc. concentrated HNO_3 and allowed to stand three days. The test tube was then filled with distilled water, shaken thoroughly to separate the spicules from the organic debris, and allowed to settle for several hours. Most of the acid was then decanted

off and replaced by fresh water, and the process was repeated. After washing in this manner three times with water and once with 95% alcohol, fresh alcohol was added and the tube shaken to suspend the spicules. Drops of this alcohol containing spicules were then placed on cover glasses, dried by igniting the alcohol, and mounted on a slide with a drop of balsam.

The chemical methods used in analysis of the lake waters have already been described by Juday and Birge (1914, 1930, 1933). All analyses are expressed as mgms. per liter except transparency and conductivity. Transparency is expressed as the greatest depth in meters at which a standard Secchi disc is visible. No reading for transparency is given for several of the shallow lakes because the disc was plainly visible at the bottom. Conductivity is expressed as reciprocal megohms.

DATA

In all, 127 lakes and bogs, and 17 streams were examined, of which 103 lakes and 15 streams showed sponge faunas. 1389 sponges were examined microscopically in addition to a large number of specimens readily recognized without microscopic examination. The collections include 10 species, of which one, *Ephydatia everetti* (Mills), is a new report for the state and, so far as the author is able to determine, for the region west of the Alleghany mountains. This species, in addition to twelve species listed by Smith (1921) as occurring in Wisconsin, makes thirteen species of Spongillidae known to occur in the state. The species collected by the author were *Spongilla lacustris* (Linnaeus), *Spongilla fragilis* Leidy, *Spongilla ingloniformis* Potts, *Ephydatia mülleri* (Lieberkuhn), *Ephydatia everetti* (Mills), *Tubella pennsylvanica* Potts, *Heteromyenia argyrosperma* Potts, *Heteromyenia repens* Potts, *Heteromyenia ryderi* Potts, and *Carterius tubisperma* Mills. Of the species listed by Smith, three were not found by the author in the region studied, *Ephydatia fluviatilis* (auctorum), *E. crateriformis* (Potts), and *Carterius latitentus* Potts.

Table 1 gives the data for lakes and bogs, and Table 2 for the streams in which sponges were found. Lakes and streams in which no sponges were found have been omitted from the tables since in most cases failure to find sponges may have been due to inadequacy of collecting equipment. In two types of lakes only was the author convinced that failure to find sponges was due to their absence. This was the case in certain small senescent bogs choked with algae, and without sufficient exposure to wind to provide water movement; and in lakes of low transparency, regular shore line, and sand or gravel bottom, in which the effect of wave action extended deeper than light adequate for sponge growth. In addition to the chemical data presented in Table 1, the waters of the lakes from which sponges were collected have been analyzed for plankton, ammonia, organic N, NO_2, NO_3, total N, phospho-

rus, chlorine, and, in some, calcium. Since, however, not the slightest correlation appeared between any of these constituents and the occurrence of sponges, these analyses have been omitted. No chemical analysis is given for the streams, since the water is essentially similar to that of the lakes drained by them. Additional chemical data, as well as the description of the lakes studied, may be found in the works of Juday (1914), Juday and Birge (1930), or Birge and Juday (1934).

In Table 2, under the sponges collected, the fourth column is headed "*S. lacustris* (atypical). This heading is used to designate a type of *Spongilla lacustris* in which the dermal spicules, characteristically microspined, are either exceedingly slender and without microspines, or entirely wanting. This form was, at first, diagnosed as *Spongilla aspinosa* Potts 1880. As the work progressed, however, evidence accumulated which seemed to indicate that such Wisconsin specimens are not to be regarded as a distinct species but as variants of *S. lacustris*. Forms with attenuated skeletal elements were encountered in other species also, notably in *Tubella pennsylvanica*. In these cases, however, there was no sharp line of demarcation—such as presence or absence of spines—by means of which the variants might be certainly distinguished, so no attempt has been made to separate them in the table. A discussion of these forms is reserved until after the chemical data have been presented.

INTERPRETATION AND DISCUSSION OF DATA

An analysis of the data shown in Tables 1 and 2 shows that certain species are frequently associated whereas others have not been found together. The frequency of association of the various species is shown in Table 3 compiled from Tables 1 and 2.

Table 3 shows that of the 29 times *Ephydatia mülleri* was collected, it was found associated 27 times each with *Spongilla fragilis* and *S. lacustris,* and only 7 times with *Tubella pennsylvanica*. *Spongilla fragilis* was taken 55 times, of which it was associated with *Ephydatia mülleri* 27 times, with *Spongilla lacustris* 45 times, with *Tubella pennsylvanica* 16 times, and occurred alone 8 times. At the other extreme, the atypical form of *Spongilla lacustris*, which was collected from 20 lakes, occurred 11 times with *Tubella pennsylvanica*, once with *Spongilla ingloviformis*, 10 times with *Ephydatia everetti*, and 5 times alone, but was never found coexistent with *Ephydatia mülleri, Spongilla fragilis,* or the typical forms of *S. lacustris*. Two distinct and mutually exclusive association groups thus appear among the sponges, one consisting of *Ephydatia mülleri* and *Spongilla fragilis,* the other of *Ephydatia everetti* and the atypical *Spongilla lacustris*. Such a distribution indicates the probability that certain environmental factors, necessary for one group of sponges, are prohibitive to another.

TABLE 1

Lakes	Disc	O_2	Free CO_2	Fixed CO_2	pH	SiO_2	Conductivity	Residue	Color	E. mulleri	S. fragilis	S. lacustris	S. lacustris (atyp.)	T. pennsylvanica	S. ingloviformis	E. everetti	H. argyrosperma	H. repens	H. ryderi	C. tubisperma
Allequash	1.5	9.4	—1.75	16.5	8.6	5.2	61	56.8	36	..	*	*	..	..	..	..	..	..	..	..
Anna	1.3	.....	2.0	2.0	6.5	0.45	19	41.8	74	..	*	*	..	*	..	..	..	..	..	..
Anne	2.3	9.7	1.5	2.5	5.1	0.3	12.2	18.2	24	..	..	..	*	..	..	..	..	..	..	..
Arborvitae, Big	.....	10	—1.5	21.2	8.4	3.3	88	70.5	24	*	*	*	..	..	..	..	..	..	..	..
Bass (by N. Pickerel)	.....	8.0	2.0	2.5	5.3	0.2	13.5	....	6	..	..	..	..	..	*	*	..	..	..	..
Bear	3.0	9.4	0.5	3.5	5.9	0.8	13	20.7	28	..	..	*	..	*	..	*	..	..	..	..
Big	2.0	8.4	—1.2	20.3	8.3	4.0	96	70.2	25	*	*	*	..	..	..	..	..	..	..	..
Bog (on Black Oak Road)	.....	8.1	7.0	22.0	7.3	19	87	71.5	33	..	*	*	..	..	..	..	..	..	..	..
Bog (by Little Dear Lake)	.....	.....	......	......	.....	.....	.....	....	.....	..	..	..	*	*	..	..	..	..	..	..
Bog (by Buck Lake)	.....	.....	......	......	.....	.....	.....	....	.....	..	..	*	..	*	..	..	..	..	*	..
Boulder	1.9	7.7	3.0	12.1	7.2	7.0	56	50.4	64	*	*	*	..	..	..	..	..	..	..	..
Bug	1.8	7.1	2.5	4.0	6.5	1.0	17.7	27.9	53	..	*	..	..	*	..	..	..	*	..	..
Camp	5.3	6.9	1.5	0.5	5.8	Trace	11.9	11.1	13	..	..	..	*	*	..	*	..	..	..	..
Carlin	7.5	7.9	1.0	1.4	6.4	Trace	12.5	15.2	8	..	..	..	*	..	..	..	..	..	..	..
Clear (Oneida Co.)	8.1	8.6	1.0	4.5	6.1	Trace	17	17.1	0	..	..	..	*	..	..	..	..	..	..	..
Crane	4.5	8.1	1.0	2.5	5.6	0.15	14.9	16.3	15	..	..	..	*	..	..	*	..	..	..	..
Crawling Stone	3.0	7.2	1.5	11.3	7.4	1.2	58	36.1	0	..	*	*	..	..	..	..	..	..	..	..
Crystal	12.7	8.2	1.0	0.5	5.1	Trace	11	29.4	0	..	..	..	..	..	..	*	..	..	..	..
Curtis	4.5	.....	2.3	0.6	6.2	Trace	13	12.5	8	..	..	..	..	..	*	*	..	..	..	..
Dam	0.9	6.1	2.0	6.0	6.7	5.0	33	52.9	94	*	*	*	..	..	..	..	..	..	..	..
Elizabeth	.....	.....	2.3	3.0	5.0	0.7	11	15.8	6	..	..	..	..	*	*	*	..	..	..	..
Ellerson, Middle	5.0	8.5	1.2	1.3	6.4	Trace	11.1	19.1	0	..	..	..	..	*	..	..	..	..	..	..
Ellerson, West	....	10.5	4.3	22.1	8.5	8.0	95	77.6	26	..	*	*	..	..	..	..	..	..	..	..
Flato	.....	9.4	1.7	4.5	6.1	Trace	7.5	16.5	16	..	..	..	..	..	..	*	..	..	..	..
George (N. of Winchester)	3.0	8.8	1.0	4.0	6.2	0.3	20	33.5	43	..	*	*	..	*	..	..	..	..	..	..
George (Black Oak Road)	.....	8.4	3.0	9.0	6.7	1.0	26	....	14	..	..	*	..	..	..	..	..	..	..	..
Grassy	.....	6.5	6.2	10.2	6.8	4 0	38	44.6	53	*	*	*	..	*	..	..	*	*	..	..
Grassy (by Wishau)	.....	6.7	2.0	3.5	6.2	0.5	12	19.7	8	..	..	..	..	*	..	..	..	..	..	..
Gresham, Upper	8.2	6.7	3.4	16.9	7.0	5.6	74	61.0	12	..	*	..	..	..	..	..	..	..	..	..
Gunlock	1.8	8.1	1.2	16.5	7.4	4.0	68	57.3	32	..	*	..	..	..	..	..	..	..	..	..
Harvey	0.75	8.1	0.5	6.9	7.6	3.6	35	79	202	..	*	*	..	*	..	..	*	..	..	..
Helen (by Winchester)	1.6	6.8	4.0	2.5	6.0	0.4	18.5	39.2	97	..	..	*	..	*	*	..	..	..	..	..
Helmet	0.8	.....	5.0	2.0	5.6	4.4	19	71	268	..	..	..	..	*	*	..	..	..	..	..
High	1.9	10.2	0.8	23.0	7.4	6.0	85	66.9	22	..	*	*	..	..	..	..	..	..	..	..
Hurrah	5.0	8.8	2.0	3.0	6.4	0.3	18	20.8	15	..	..	*	..	*	..	..	..	..	..	..
Irving	.....	8.3	2.0	13.0	7.2	7.2	56	56.8	32	..	*	*	..	..	..	..	..	..	..	..
Joyce	4.0	7.3	1.7	0.7	6.0	Trace	9	15.3	11	..	..	..	*	..	..	*	..	..	..	..
Katinka	6.0	7.8	0.5	1.7	6.1	Trace	12.9	17.1	10	..	..	..	*	..	..	..	..	..	..	..
Larry	6.5	9.6	1.2	0 7	5.1	Trace	11	18.6	8	..	..	..	*	*	..	*	..	..	..	..
Little Arborvitae	2.6	7.8	2.0	21.5	7.4	4.0	87	73.5	26	*	*	*	..	..	..	..	..	..	..	..
Little Crooked	2.2	7.0	2.0	23.0	7.6	3.0	92	67.1	22	..	..	*	..	..	..	..	..	..	..	..
Little Horsehead	.....	.....	......	11.1	7.0	2.0	52	58.1	58	*	*	*	..	*	..	..	..	..	..	..
Little John, Jr.	2.3	7.3	2.0	0.55	5.7	Trace	9.5	19.1	16	..	..	..	..	*	*	..	..	..	..	..
Little Long	1.5	7.6	2.2	6.5	7.1	2.4	28	50.8	68	..	*	*	..	*	..	..	..	..	..	..
Little Maimie	3.0	8.4	2.0	1.25	5.4	0.25	9.8	20	16	..	..	..	..	*	*	*	..	..	..	..
Little Muskelunge	1.9	8.2	0.6	18.5	8.1	6.6	78	61.9	43	..	*	..	..	..	..	..	..	..	..	..
Little Papoose	2.3	8.1	1.0	20.0	7.0	2.5	78	68.6	49	*	*	*	..	..	..	..	..	*	..	..
Little Pickerel	1.1	7.6	4.5	8.0	6.8	12.0	28	70.6	108	..	..	*	..	*	..	..	..	..	..	..
Little Rice	.....	10.3	1.6	8.4	7.2	7.0	45	45.3	43	*	*	*	..	*	..	..	*	..	..	..
Little Rock	.....	5.6	2.0	0.7	5.7	Trace	11	14.9	8	..	..	..	*	*	..	*	..	..	..	..
Little Rudolph	3.5	7.5	1.6	0.8	5.9	Trace	8.2	13.8	5	..	..	..	*	*	..	..	..	..	..	..

TABLE 1 *(Continued)*

Lakes	Disc	O_2	Free CO_2	Fixed CO_2	pH	SiO_2	Conductivity	Residue	Color	F. mulleri	S. fragilis	S. lacustris	S. lacustris (atyp.)	T. pennsylvanica	S. ingloviformis	E. everetti	H. argyrosperma	H. repens	H. ryderi	C. tubisperma
Little St. Germaine	1.7	10.7	—0.5	13.4	7.3	0.7	58	42.7	14	*	*	..	..	..	..	..	..	..	..	..
Long (by Crystal)	4.4	7.6	1.5	1.5	5.5	0.35	9.5	14.2	20	..	..	..	*	..	..	*	..	..	..	..
Louise	.....	6.8	3.0	1.7	5.8	0.3	10	16.5	8	..	..	..	..	*	*	*	..	..	..	..
Lucy	2.3	8.3	0.7	2.2	8.3	1.6	17	28.5	32	..	..	*	..	*	..	..	..	..	..	..
Lynx	.....	6.5	2.2	1.0	6.1	Trace	16.5	24.9	30	..	..	*	..	..	..	..	..	..	..	..
Malby	.....	.....	1.5	0.9	6.0	0.25	12.5	13.8	15	..	..	..	..	*	*	*	..	..	..	..
Mann	.....	8.8	—2.7	25.55	8.0	6.0	105	93.2	20	..	*	..	..	..	..	..	..	..	..	..
Mary (by Winchester)	1.7	6.0	5.5	3.0	5.4	1.0	19.5	51.3	132	..	..	*	..	*	*	..	..	..	..	..
Mary (by Papoose)	3.5	8.8	2.5	3.0	5.7	0.25	11.5	15.4	14	..	..	..	*	..	..	..	..	..	..	..
Midge	3.2	6.9	1.5	2.5	5.4	Trace	11.0	20.5	35	..	..	..	*	*	..	..	..	..	..	..
Mud	3.0	7.2	2.0	6.0	6.3	0.3	17	25.8	45	..	..	*	..	..	..	..	..	..	..	..
Muskelunge	3.5	8.4	1.2	10.5	7.4	0.3	42	31.2	5	..	..	*	..	..	..	..	*	..	..	..
Muskelunge (by Pickerel)	0.5	6.6	......	14.9	6.9	10.0	62	86.4	105	..	*	..	..	..	..	..	..	..	..	..
Nebish	7.3	8.2	1.5	4.5	6.6	0.4	19	21.9	5	..	..	*	..	..	..	*	..	..	..	..
Nellie	1.3	5.0	1.2	0.7	6.5	0.5	10.8	26.5	118	..	..	..	..	*	..	..	..	..	..	..
Nixon	.....	8.5	1.0	13.0	7.1	5.0	47	66.6	118	*	*	*	..	..	..	..	..	..	..	..
No-see-em	1.0	7.3	5.0	4.0	5.2	0.5	19	50.0	148	..	..	*	..	*	*	..	..	..	..	..
Oswego	2.7	9.0	2.5	2.5	6.2	0.4	13	17.9	18	..	..	..	*	*	..	*	..	..	..	..
Ox bow	1.1	7.2	1.7	9.0	6.9	1.5	34	61.2	97	..	*	*	..	*	..	..	..	..	..	..
Papoose	2.8	8.0	1 2	23.5	7.7	1.6	88	74.0	18	*	*	*	..	..	..	..	..	..	..	..
Pardee	1.1	.....	......	14.0	7.6	2.5	65	65.9	68	..	*	..	..	..	..	..	..	..	..	..
Perch (Ruth)	5.5	6.4	1.4	0.5	5.9	Trace	9.5	14.3	20	..	..	..	*	*	*	*	..	..	..	..
Pickerel	0.9	7.7	......	15.5	7.1	5.5	64	74.3	53	..	..	*	..	*	..	..	*	..	..	..
Plum	4.7	8.0	0.8	16.4	8.0	4.6	73	58.0	16	..	..	*	..	..	..	..	..	..	..	..
Presque Isle	3.8	8.8	—1.0	27.5	8 3	0.8	101	71.7	14	..	*	*	..	..	..	..	..	..	..	..
Puddle	.....	4.4	2.5	6.5	6.6	2.0	54	50.0	43	*	*	*	..	*	..	..	..	..	..	..
Rice, Big	1.7	.....	......	16.3	7.3	5.3	70	54.2	40	*	..	*	..	..	..	..	..	..	..	..
Rice (by Plum)	.....	4.0	13.9	17.1	6.6	8.2	70	65.4	88	*	*	*	..	..	..	..	..	..	..	*
Rock	2.1	8.5	0.5	10.0	7.2	0.6	37	43.7	32	..	..	*	..	..	..	..	..	..	..	..
Rose	1.1	8.4	1.8	2.7	6.7	2.5	25	53.9	128	.	..	*	..	*	..	..	..	..	..	..
Rudolph	1.8	7.4	1.5	2.5	5.6	0.3	17	34.0	55	..	..	*	..	..	..	..	..	..	..	..
Shishebogoma	3.0	8.6	1.3	14.7	7.3	4.0	67	54.0	16	..	*	..	..	*	..	..	..	..	..	..
Street	5.0	7.2	1.8	0.7	5.9	Trace	10	14.5	0	..	..	..	..	..	..	*	..	..	..	..
Stella	.....	8.7	1.7	15.3	7.3	8.8	66	66.8	101	..	*	*	..	*	..	..	..	..	..	..
Sunday	4.0	. .	1.3	1.6	6.7	0.3	13	18.9	0	..	..	..	*	*	..	..	..	..	..	..
Tadpole	0.9	7.8	1.0	2.7	5.6	0.9	20	57.3	101	..	..	*	..	*	*	..	..	..	..	..
Tamarack	1.7	6.3	3.0	13.4	7.1	2.1	67	75	101	*	*	*	.	*	..	..	..	*	..	..
Trilby (1931)	.....	8.0	1.5	1.0	7.0	0	13	14.2	14	..	..	..	*	*	..	..	..	..	..	..
Trilby (1934)	.....	.....	1.4	2.1	7.5	0.5	14	18.2	12	..	..	*	..	*	*	*	..	..	..	..
Trout	5.0	8.5	2.0	18.5	7.5	7.3	75	59.5	6	*	*	*	..	..	..	..	..	..	..	..
Turtle	2.2	4.7	1.5	7.0	7.4	2.0	56	67.9	50	*	*	*	..	..	..	..	..	..	..	..
Twin, N.	.....	.....	4.0	11.0	7.2	13.0	31	.....	.....	..	..	*	..	..	..	..	..	..	..	..
Vieux Desert	1.3	8.0	1.1	16.4	7.2	2.4	64	58.0	32	..	*	..	..	..	..	..	..	..	..	..
Weber	9.3	8.3	1.0	2.0	5.8	0.1	9.5	12.2	0	..	..	..	..	..	..	*	..	..	..	..
White Birch	3.5	8.8	0.7	13.2	7.6	4.5	56	51.2	60	..	*	*	..	..	..	..	..	..	..	..
White Sand	3.7	8.4	1.4	15.9	7.7	5.4	57	51.1	16	*	*	*	..	..	..	..	..	..	..	..
Wild Cat	2.3	7.9	0.3	33.2	8.3	3.6	118	88.7	26	..	*	*	..	..	..	..	..	..	..	..
Wishau	.....	7.4	1.5	2.0	6.0	0.3	10	15.0	0	..	..	..	*	*	..	*	..	..	..	..
Wolf	2.2	8.5	4.5	26.0	8.0	2.6	90	87.2	32	..	*	..	..	..	..	..	..	..	..	..
Walker	2.2	8.4	2.0	1.5	5.8	0.2	8	22.4	35	..	..	..	*	..	..	*	..	..	..	..
Yolanda	1.0	6.8	4.2	2.5	5.5	0.4	15.2	43.3	132	..	..	*	..	*	*	..	..	..	..	..

TABLE 2

Stream	Character	E. mulleri	S. fragilis	S. lacustris	T. pennsylvanica	H. argyrosperma	H. repens	H. ryderi	C. tubisperma
Allequash inlet	Spring fed, bog margin	..	*	*	..	..	..	..	..
Allequash outlet	Gentle current, bog margin	*	..	*	..	..	..	..	..
Big Lake outlet	Wide, shallow, over gravel bottom	*	*	*	..	..	..	..	..
Little Horsehead outlet	Rapids, rock bottom	*	..	*	..	*	..	..	*
Little St. Germaine outlet	Ponded by a dam, little current	*	*	..	..	..	..	..	..
Manitowish River									
Below Little Rice Lake	Sluggish, boggy	..	*	*	*	..	..	..	..
Below Boulder Lake	Rapids, rock bottom	*	*	*	..	..	..	..	..
Mann Lake outlet	Riffel, rock bottom	*	*	*	..	..	*	..	*
Mud Creek	Ponded by dam, little current	*	*	*	*	*	..	..	..
Plum Lake outlet	Shallow, gentle current over gravel bottom	..		*	..	..	..	..	..
Presque Isle outlet	Both ponds and riffels	..	*	*	..	..	..	..	..
Rice Creek	Ponded by dam	*	*	*	*	*	..	..	..
Trout Lake inlet	Spring fed, gentle current, bog margin	*	*	*	..	..	..	*	..
Trout Lake outlet	Current over gravel bottom, wooded margin	..	*	*	..	..	..	..	..
Turtle Lake outlet	Current over gravel and pebbles	..	*	*	..	*	..	..	..
Wisconsin River									
above dam	Sluggish with much wood debris	*	*	*		*	..	..	..
Otter Rapids	Strong current over rock bottom	*	*	..	..	..	..	..	..

TABLE 3. Showing the frequency of association of the species of *Spongillidae* collected

No. of times collected	Species	E. mulleri	S. fragilis	S. lacustris	T. pennsylvanica	S. ingloviformis	E. everetti	S. lacustris (atypical)	H. argyrosperms	H. repens	H. ryderi	C. tubisperms
29	E. mulleri	..	27	27	7	..	..	..	6	4	1	3
55	S. fragilis	27	8	45	16	..	..	..	6	4	1	2
70	S. lacustris	27	45	11	27	12	2	..	10	5	2	3
49	T. pennsylvanica	7	16	27	3	14	11	11	6	3	1	..
15	S. ingloviformis	..	..	6	14	.	7	1	..	..	..	..
22	E. everetti	..	..	2	11	7	4	10	..	..	..	..
20	S. lacustris (atypical)	..	..	..	11	1	10	5	..	..	..	..
10	H. argyrosperms	6	6	10	6	..	..	..	..	1	..	1
5	H. repens	4	4	5	..	..	..	..	..	..	..	1
2	H. ryderi	1	1	2	..	..	..	..	..	..	..	1
3	C. tubisperma	3	2	3	..	..	..	..	.	1	1	..

The typical form of *Spongilla lacustris,* although overlapping slightly the ecological range of *Ephydatia everetti,* is never found coexistent with the atypical form, and shows a decided preference for the conditions favoring *Ephydatia müller*i and *Spongilla fragilis. Tubella pennsylvanica* is the only species found coexisting with all of the other forms, a fact which suggests

that its distribution is controlled by a still different complex of environmental factors than those which separate *Ephydatia mülleri* and its associates from *Ephydatia everetti* and its.

Spongilla ingloviformis presents still another set of problems. Although never taken with *Ephydatia mülleri* or *Spongilla fragilis,* it can not be classed with *Ephydatia everetti* and the atypical forms of *Spongilla lacustris* because of its low association with the latter and only moderately frequent association with the former. On the other hand, its association with *Tubella pennsylvanica* is very high, 13 times out of 15.

The Heteromyenias are associated with *Spongilla lacustris,* and usually also with *Ephydatia mülleri* and *Spongilla fragilis,* although the low frequency of their collection indicates the requirement of some condition not demanded by the more common forms.

In addition to the question of factors controlling the presence or absence of the various species, there is also the problem of possible factors producing the marked structural variations already mentioned as occurring in *Tubella pennsylvanica.* Since its first description, *Tubella pennsylvanica* has been known as a highly variable species. It was, then, not surprising that the author should find forms so divergent that, were there no intergradents, they might readily be accepted as distinct species. The "typical", or usually described and figured form of *T. pennsylvanica* is characterized by gemmules thickly studded with inequaebirotulate spicules arranged at right angles to the gemmule wall, and having rotules with entire margin (Fig. 18). The shaft of these birotules is enlarged at the end adjoining the larger, or proximal, rotule, and the entire structure is surrounded by a crust of thickly spined acerates. The most common variation from this "typical" form was a sponge having gemmule walls containing very few spicules. The few inaequibirotulates present consisted of a minute knob shaped distal rotule scarcely larger than the shaft, and a proportionately long and exceedingly slender shaft (Figures 17, 19, 20 and 21). In some cases the proximal rotule was apparently not silicified, its position being indicated merely by an indistinct outline in the structure of the organic matrix. In other specimens many of the scattered inaequibirotulates were not standing upright but lay on their sides. The acerate spicules surrounding the gemmule were also sparse, so that the gemmule wall had the appearance of being composed, largely, of a hyaline leathery material like the gemmule walls of *Spongilla lacustris.* The vegetative parts of such sponges were frequently well developed. The skeletal spicules were extremely long and slender, (Fig. 22), and sometimes curved, so that the sponge skeleton had the appearance of a mass of tangled barb wire. Specimens of this kind were encountered in the bog near Little Deer Lake, and in the following lakes: Camp, Middle Ellerson, Grassy (Near Wishau), Larry, Little John Junior, Little Maimie, Little Rock, Little Rudolph, Louise, Malby,

Midge, Oswego, Perch, Sunday, Trilby (1932), and Wishau. Specimens somewhat less atypical, but regarded as intermediate in skeletal development, appeared in lakes Elizabeth, Hurrah, Nellie, No-see-em, and Trilby (1934): whereas, even among specimens readly recognized as *Tubella pennsylvanica,* there appeared great variations in the degree of development of the gemmule spicules. It was, furthermore, observed that wherever these unusual forms appeared, all of the specimens from that lake showed the same variation to approximately the same degree, suggesting that these variations were due to some environmental condition unfavorable to skeletal development. And, finally, it will be observed that the lakes in which these atypical Tubellas occurred include all of the lakes in which this species is associated with the atypical forms of *Spongilla lacustris,* 9 of the 11 lakes in which it is associated with *Ephydatia everetti,* and 4 lakes in which it is the only species present. This being the case, it appears probable that the same environmental factors which so sharply separate the atypical forms of *Spongilla lacustris* from *Ephydatia mülleri* and its associates may also produce skeleton-poor Tubellas.

In analyzing environmental data one must, then, except at least three different sets of factors affecting the distribution of the sponges: (1) factors favoring *Ephydatia mülleri, Spongilla fragilis,* and *Spongilla lacustris* but inimical to *Ephydatia everetti;* (2) factors inimical to *Ephydatia mülleri* and *Spongilla fragilis,* tolerated to a slight degree by *Spongilla lacustris,* but favorable to *Ephydatia everetti* and the atypical forms of *Spongilla lacustris* and probably also affecting the spicule development in *Tubella pennsylvanica;* and (3) factors favoring *Spongilla ingloviformis* and probably also *Tubella pennsylvanica,* but either inimical or indifferent to the remaining forms.

In seeking an explanation of animal distribution in terms of the physical and chemical environment there are three ways in which data are frequently handled: (1) the entire range of each factor known to be tolerated by each species may be compared, (2) the frequency of each species in each type of environment may be compared, and (3) the optimum environment for each species may be compared. In the following pages all three methods are employed. Except in the discussion of current, the data on lakes and bogs (Table 1) only are used.

Figure 1 represents diagramatically the range of environmental conditions from which each species was collected. The lines represent the entire range of conditions found in the 127 lakes studied whereas the black part of each line represents the range through which the species in question was found. Tables 4 to 13 inclusive give the frequency of occurrence of each species in the various concentrations of environmental factors under consideration, and Table 14 shows the range of conditions under which each species was found in greatest luxuriance and abundance.

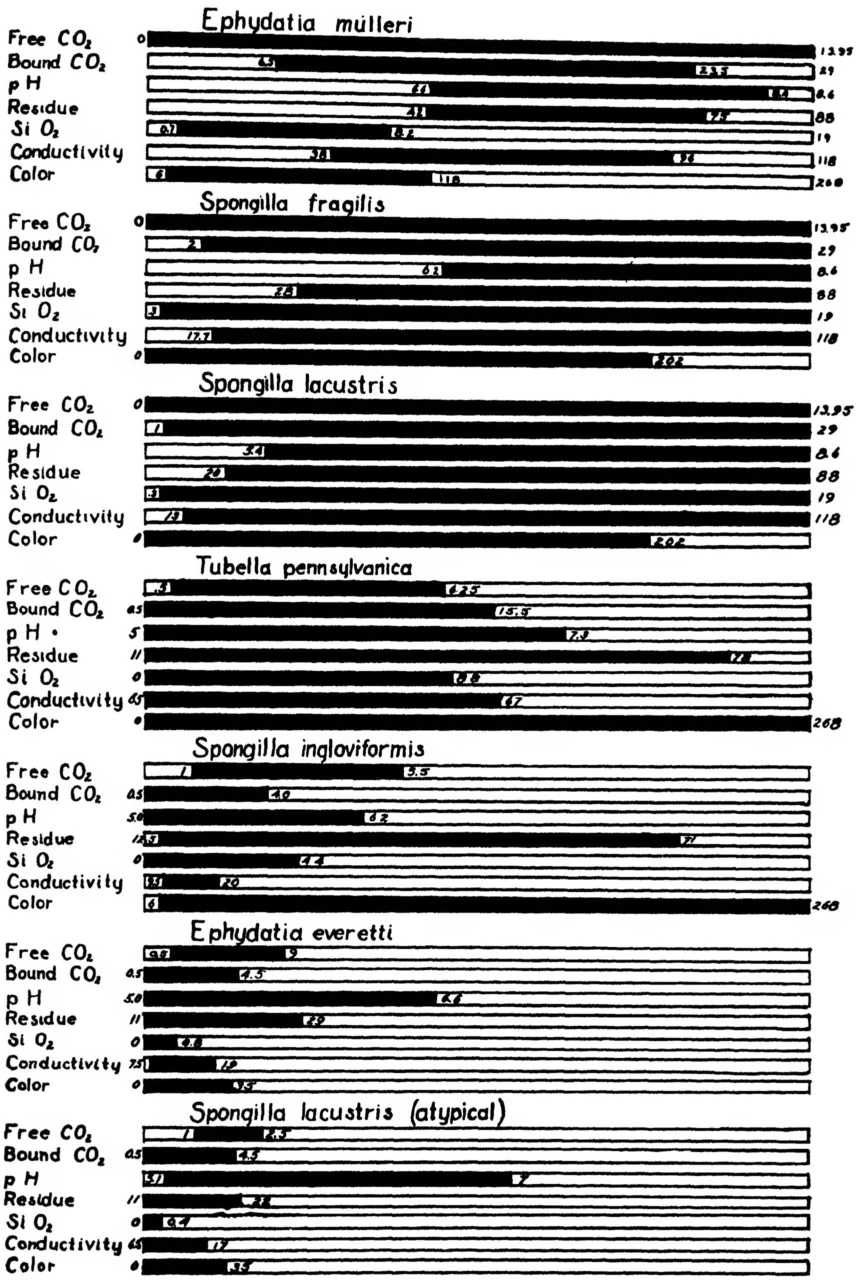

FIGURE 1. Diagram showing the distribution of fresh-water sponges with reference to the physical and chemical factors of the water. The entire line represents the range of each condition found in the series of lakes studied. The black part of the line represents the range from which the species of sponge under consideration was collected.

DISTRIBUTION OF SPECIES WITH RESPECT TO THE PHYSICAL AND CHEMICAL ENVIRONMENT

TRANSPARENCY OF THE WATER

TABLE 4. Distribution of sponges with reference to the transparency of the water

Sponge	Transparency as meters visibility of Secchi's disc.							
	0–1	1.1–1.5	1.6–2	2.1–3	3.1–4	4.1–5	5.1–6	Over 6
E. mülleri	1	.	5	4	1	1	.	.
S. fragilis	3	6	8	10	4	1	.	.
S. lacustris	6	6	9	12	4	3	.	1
T. pennsylvanica	6	6	4	7	3	1	3	1
S. ingloviformis	4	.	2	2	.	1	1	.
E. everetti	.	.	.	4	1	4	3	4
S. lacustris (atypical)	.	.	.	3	5	2	3	3
Lakes	10	9	14	24	11	13	5	8

In considering the relation of sponge distribution to the transparency of the water, the data in the above table show little except the absence of *Ephydatia everetti* and the atypical *Spongilla lacustris* from the less transparent waters. Transparency of the water then appears to be of little importance in determining whether any species except the two mentioned shall occur in any given lake or not. It does, however, appear from field observations, that transparency may be of considerable importance in determining the depth, and location with respect to shade, at which any species may be found. Thus, in waters of low transparency, like those of Harvey, Little Pickerel, or Rose, *Spongilla lacustris* was found, frequently in great abundance, growing from a depth of a few centimeters to a half meter up to the surface in unshaded situations; whereas in more transparent waters, like those of Little Papoose, Nebish, or White Sand, the same species was collected near the surface in partially shaded situations, as on the submerged stems and roots of Chamaedaphne shrubs, or, at a depth of 1 to 1.5 meters in less shaded situations. The relation of *Ephydatia mülleri* to light appears to be essentially the same as for *Spongilla lacustris*. *S. fragilis,* on account of its ability to grow well on the under side of the substrate, is more frequently found under logs in unshaded transparent waters.

Ephydatia everetti and the atypical *Spongilla lacustris* are apparently light positive forms, occurring in exposed situations in the most transparent waters at depths of from 0.2 meters to over 3 meters. In Weber and Bass lakes *Ephydatia everetti* reached its maximum abundance at a depth of 1.5 meters and was still common at 2 meters. In Weber it was still found at 3 meters. In Louise, great festoons of this form were visible at a depth of 2.5 to 3 meters, in Crystal it was collected at 3.5 meters, while in Larry

and Joyce both *Ephydatia everetti* and the atypical *Spongilla lacustris* persisted to a depth of about 3.5 meters. The record for Crystal Lake, 3.5 meters, is the greatest accurately measured depth from which the author has obtained any sponge.

Tubella pennsylvanica and *Spongilla igloviformis* are both found in light of low intensity. Although collected from some of the most transparent waters it was observed that, in such situations, both species invariably occurred in the under side of the support or actually embedded in the organic deposits of the bottom. Thus, in Little John Junior, *Tubella pennsylvanica* is recorded as found on the under side of wood partially covered by the decomposing organic matter of the bottom, and in Camp Lake the same sponge was found on the embedded parts of sticks pulled from a bottom which emitted gas bubbles when the sticks were removed. *Spongilla igloviformis* was taken from the under sides of logs and boards resting on the bottom in Curtis and Little Mamie lakes, while in Malby it was found in abundance in similar locations, and also on both the upper and lower sides of logs brought up from a depth of 1.5 meters but entirely concealed from the surface by a rank growth of filamentous algae which rose, in billows, almost to the surface. In lakes of low transparency, like Helmet, Tadpole, and Yolanda, the same two species occurred on the upper as well as the lower surfaces of their supports and only a few centimeters below the surface. One curious fact is that even these light negative forms were never collected below the limit of light penetration as judged by the visibility of Secchi's disc, and that the sponge collected at the greatest depth was the light positive form, *Ephydatia everetti*.

COLOR AND ORGANIC CONTENT OF THE WATER

Color of water, although often closely associated with transparency, is, nevertheless, a distinct factor. A decreased transparency may result from either color or suspended matter, whereas color is the result of substances, usually organic, in solution.

Birge and Juday (1932) have shown that whereas as much as 30 to 39% of the solar energy with the sun at zenith is transmitted to a depth of one meter in lakes such as Crystal, Weber, or Clear, that in Turtle Lake, with a color of 68, only 6.4% reaches a corresponding depth, while in still darker lakes, Little Pickerel and Helmet with colors of 108 and 260, the transmission of solar energy at a depth of 1 meter drops to 3.5% and 1% respectively. Furthermore there is not only a decrease in the total amount of energy transmitted, but the various wave lengths are absorbed at different rates depending upon the color of the water, so that the qualitative effect upon the light transmitted by a highly colored water may be very different from that of a colorless but turbid water of the same transparency.

That the effect of color on sponge life is not simply a matter of decreased

light is evident, since waters of high color were usually rich in sponges, whereas waters of little or no color, but of low transparency, even though the turbidity was due to plankton, were invariably poor to lacking in sponge life.

As the color of water is usually due to dissolved organic matter, it is roughly proportional to organic content, and so indicates the amount of nutriment available to such animals as sponges. Because of this correlation the full data for organic content have not been included in Table 1. Table 5 shows, however, that the effect upon sponge distribution of color and of total organic matter, is practically the same. With an increase in color, then, the food available to sponges is usually increased, whereas the light available is qualitatively altered and quantitatively decreased.

TABLE 5. Distribution of Sponges with reference to Color and Total Organic Content of the water

Sponge	Degree of color of water								
	0-10	11-20	21-30	31-40	14-50	51-75	76-100	101-150	over150
E. mülleri	1	3	3	1	4	3	2	2	.
S. fragilis	3	7	5	6	7	8	3	4	1
S. lacustris	5	6	9	7	5	8	4	9	1
T. pennsylvanica	9	9	1	2	3	6	2	9	2
S. ingloviformis	4	4	.	.	.	.	1	4	1
E. everetti	11	9	1	1	.	.	.	.	.
S. lacustris (atypical)	8	7	1	2	.	.	.	.	.
Lakes	36	23	14	14	6	13	4	11	2

Sponge	Total Organic content as mgms. per liter						
	3.5-5	5.1-7	7.1-10	10.1-15	15.1-25	25.1-40	Over50
E. mülleri	.	.	2	6	8	3	.
S. fragilis	.	2	2	14	16	8	1
S. lacustris	.	3	4	15	16	13	1
T. pennsylvanica	3	5	7	6	8	11	2
S. ingloviformis	3	1	2	2	.	4	1
E. everetti	6	4	9	3	.	.	.
S. lacustris (atypical)	2	4	9	3	1	.	.
Lakes	6	6	19	24	25	14	2

A comparison of Table 5 and Fig. 1, shows that, except in case of *Ephydatia everetti* and the atypical *Spongilla lacustris,* color, or the corresponding organic content, have no apparent effect in limiting the distribution of these sponges studied. The absence of *Ephydatia mülleri* from 8 lakes having colors above 118, and from 10 lakes having colors below 6, can not be regarded as more than suggestive, since, of these lakes, only two, Crawling Stone and Harvey, were not also lower in either or both conductivity and silica than any water from which this species was taken.

Although apparently not important in determining the presence or absence

of any species, except possibly *Ephydatia everetti,* color (or the accompanying high organic content) is of primary importance in determining the abundance of most species of sponges in waters otherwise suitable, as shown by examination of Table 15, in which the optimum habitats are compared. Here, it will be observed that three species, *Ephydatia mülleri, Spongilla fragilis,* and *S. lacustris,* attain their finest development in waters relatively high in color (less than 30% of the lakes have colors of 40 or above), whereas the luxuriance of *Tubella pennsylvanica* appears to be almost a function of the color of the water. *Spongilla ingloviformis,* although attaining numerical abundance and extensive growth in two clear water lakes—Elizabeth and Malby—where it developed in contact with bottoms rich in organic detritus, still showed by far the most luxuriant development in the darker waters, and reached its climax in the lake of highest color—Helmet. In the clear lake waters representatives of this species appeared as delicate uniform incrustations, bright green in color, and 5 to 7 mm. thick. In the darker waters they became heavily incrusting to massive, rugose, vivid to dark green, and up to 25 mm. in thickness, (Figs. 8 and 9).

Although Helmet Lake, which supports an almost unbelievable abundance of *Spongilla ingloviformis* and *Tubella pennsylvanica,* provides scarcely any suitable substrate in the upper half meter of water which is not already occupied by one or both of these species—one frequently growing right over the other—still it is Tadpole Lake which most clearly illustrates the rôle of color in producing this wealth of sponge life.

Tadpole Lake, named for its shape, receives a small amount of seepage water through a long, gradually tapering slough which forms the "tail." The water analysis given in Table 1, which shows a color of 101, is the analysis of water from the "body". As one rows up the "tail", the water appears noticeably and progressively darker until, at a point where further progress by boat becomes impossible, the water appears fully as dark as the water of Helmet Lake. Concomitant with the increase in color is a marked increase in sponge fauna, especially *Spongilla ingloviformis* and *Tubella pennsylvanica.* These species, ordinarily thought of as characteristic of obscure corners beneath their bases of support, now appear in the open covering every snag, and plainly visible at a depth of 2 to 10 cm. beneath the surface. When brought to the surface, *Spongilla ingloviformis* invariably appears green, yet, seen through even a few centimeters of this dark water, it appears yellow to brown. No doubt it is to this color-absorbing quality of the water that these sponges owe their ability to live in exposed situations, and to the large amount of organic matter available as food, that they owe their luxuriant development.

The next darkest of the lakes (Harvey: color, 202; total organic 56.7 mgms. per 1) is given the following description in the author's field note book,

"A small lake with relatively large inlet and outlet, dark water, and bog margin. Several wagon loads of potatoes, recently dumped, float along the margin in various stages of decomposition. *Spongilla fragilis* exceedingly abundant coating sticks, dead wood, and even stones. Twigs of marginal Chamaedaphne completely coated where submerged, and, even above the water level, encrusted with dry sponge and gemmules." Although more massive specimens of *Spongilla fragilis* were found in other places, still no where else did the author find every available inch of support so completely occupied by this species as in Harvey Lake.

Little Pickerel, with color varying between 92 and 150, probably gives the nearest approach to perfection for the development of *Spongilla lacustris,* although the luxuriance of this species was practically equalled in another dark lake, Mary (color. 132).

The author does not, of course, wish to imply that color, or color and the high organic content which usually accompanies it, are alone responsible for the remarkable development of sponges in the lakes just described. The fact that of these dark lakes the sponge fauna of one was dominantly *Tubella pennsylvanica* and *Spongilla ingloviformis* of another *Spongilla fragilis,* and of the third *S. lacustris,* shows the operation of other environmental factors. Furthermore, Stella Lake, with a color of 101 and organic content of 35.5 mgms. per liter, but with a margin largely rocks and gravel, and with no protected sloughs or bays, had a relatively sparse sponge fauna despite its dark color. It is not, however, without significance, that the lakes supporting the greatest profusion of four species of Spongillidae were all dark in color.

DISSOLVED O_2 AND CO_2 IN WATER

Since dissolved O_2 and free CO_2, because of their relation to respiration, are universally conceded to be factors of primary importance for aquatic animals, they have been included here. Scrutiny of Tables 6 and 7 shows that the entire range of these factors encountered in the Wisconsin lakes under consideration falls within the limits of tolerance of all of the sponge

TABLE 6. The distribution of sponges with reference to the dissolved oxygen in the water

Sponge	Dissolved Oxygen as parts per million					
	5–5.9	6–6.9	7–7.9	8–8.9	9–9.9	10–up
E. mülleri	3	3	2	6	.	3
S. fragilis	3	5	7	19	1	5
S. lacustris	3	7	13	21	2	4
T. pennsylvanica	3	9	11	10	3	1
S. ingloviformis	.	5	3	2	.	.
E. everetti	1	2	5	7	4	.
S. lacustris (atypical)	1	2	7	5	3	.
Lakes	8	13	35	44	6	5

TABLE 7. Distribution of sponges with reference to free CO_2 in the water

Sponge	Free CO_2 as parts per million						
	0-0.9	1.0-1.5	1.6-2.5	2.6-3.5	3.6-4.5	4.6-5.5	5.6-up
E. mülleri	2	7	5	2	.	.	2
S. fragilis	10	11	12	3	2	.	3
S. lacustris	11	12	16	3	5	2	3
T. pennsylvanica	3	12	17	2	3	3	1
S. ingloviformis	.	3	4	1	2	2	.
E. everetti	1	11	9	1	.	.	.
S. lacustris (atypical)	1	12	6	.	.	1	.
Lakes	17	43	36	7	7	3	4

species studied. Neither O_2 nor CO_2 can then be regarded as influencing the distribution of sponges in the waters studied.

While, at a casual glance, Tables 6 and 7 may appear to indicate a restriction of *Spongilla ingloviformis* to certain concentrations of O_2, or of *Ephydatia everetti* to low CO_2, yet the facts of distribution, that neither of these forms was ever found associated with *Ephydatia mülleri* or *Spongilla fragilis* in nature, as well as the very small number of lakes in the part of the range from which they are absent, show that no significance can be attached to these apparent restrictions.

BOUND CO_2 IN THE WATER

Bound CO_2 is an index to the carbonate salts of the water, which consist largely of salts of Calcium. Birge and Juday (1930) show that the "hardest" water in the area studied is actually a "soft" water as compared to waters of the southern part of the state. It is, then, to be expected that the more widely distributed species, such as *Ephydatia mülleri* and *Spongilla fragilis,* would tolerate the upper limits of the bounds CO_2 found in this region.

Table 8 and Figure 1 indicate a definite restriction of *Ephydatia mülleri* to the upper part of the range of bound CO_2 found in the lakes studied, and of *Spongilla ingloviformis, Ephydatia everetti,* and the atypical *Spongilla*

TABLE 8. Distribution of sponges with reference to bound CO_2 of the water

Sponge	Bound CO_2 as mgms. per liter					
	0.5-1.0	1.1-2.5	2.6-5.0	5.1-10	11-20	21-up
E. mülleri	..	..	..	6	10	3
S. fragilis	..	1	2	9	21	10
S. lacustris	1	6	8	14	17	9
T. pennsylvanica	9	11	10	7	5	..
S. ingloviformis	4	6	4	..	..	..
E. everetti	9	8	4	..	..	..
S. lacustris (atypical)	7	9	2	..	..	..
Lakes	15	29	24	16	29	11

lacustris to very low concentrations. *Tubella pennsylvanica,* although more tolerant than the last mentioned species, is, nevertheless, restricted to the less hard waters (Fig. 1). This is in keeping with the findings of Old (1932) who describes this species as limited to waters of low temporary hardness. *Spongilla lacustris* alone seems to tolerate the entire range of bound CO_2 found in the lakes studied. While bound CO_2 may explain the separation in nature of *Ephydatia mülleri* from *Ephydatia everetti* and *Spongilla ingloviformis,* it does not explain the fact that *Spongilla fragilis* has not been found coexisting with either of these species, nor the complete separation of the microspined, from the non-microspined forms of *Spongilla lacustris.*

HYDROGEN ION CONCENTRATION OF THE WATER

TABLE 9. Distribution of sponges with respect to the pH of the water

Sponge	PH															
	5.0 5.1	5.2 5.3	5.4 5.5	5.6 5.7	5.8 5.9	6.0 6.1	6.2 6.3	6.4 6.5	6.6 6.7	6.8 6.9	7.0 7.1	7.2 7.3	7.4 7.5	7.6 7.7	7.8 8.1	8.2 up
E. mülleri	.	.	.	.	.	.	.	.	3	1	3	5	3	2	.	2
S. fragilis	.	.	.	.	.	1	.	2	3	3	4	9	6	5	3	6
S. lacustris	.	1	1	1	2	4	1	3	6	3	5	9	6	5	1	6
T. pennsylvanica	3	1	4	3	5	4	2	6	3	3	5	3	1	.	.	.
S. ingloviformis	2	2	3	2	2	2	1	.	.	.	.	.	.	.	.	.
E. everetti	4	1	2	2	6	4	2	.	1	.	.	.	.	.	.	.
S. lacustris (atypical)	2	.	3	3	4	4	1	1	1	.	1	.	.	.	.	.
Lakes	6	3	6	6	8	10	9	11	9	9	8	12	7	8	6	6

Of the species included in Table 9, *Spongilla ingloviformis* alone appears to be sharply restricted to the more acid waters, although *Ephydatia everetti* shows a marked preference for concentrations below pH 6.4 and *Tubella pennsylvanica* is lacking from the more basic waters. Old, in Michigan, found *Spongilla lacustris* and *Ephydatia mulleri* in pH 6.0 to 9.0, and *Spongilla fragilis* throughout the entire range 4.2 to 9.2. The fact that, in Wisconsin, *Spongilla lacustris* has been found extending farther into the acid range than *Spongilla fragilis,* may suggest that something other than pH is the controlling factor. pH may, however, be a factor in limiting the distribution of *Tubella pennsylvanica,* since, when collected from less acid waters, it was always found close to a mucky bottom—a position of local acidity not shown in the table.

SILICA CONTENT OF THE WATER

Because SiO_2 is the substance from which all freshwater sponges build their spicules, it may reasonably be an important factor in their distribution.

Ephydatia mülleri is apparently restricted to the higher concentration of silica. Characteristically this species has a strong skeletal development and

TABLE 10. Distribution of sponges with reference to the SiO_2 of the water

NOTE—In the determination of SiO_2, which is colorimetric, the lowest color standard used indicates 0.5 mgms. per liter SiO_2. Readings below this value are, therefore, not strictly quantitative, but depend upon the chemist's estimate of a very faint color.

Sponge	SiO_2 as mgms. per liter						
	0-trace	0.25–0.4	0.45–0.8	0.9-1.5	1.6-5.5	4.6–8	over 8
E. mülleri	.	.	1*	.	10	7	1
S. fragilis	.	1	3	3	18	13	4
S. lacustris	1	7	6	6	17	12	5
T. pennsylvanica	9	10	7	3	9	3	2
S. ingloviformis	4	5	2	2	1	.	.
E. everetti	13	7	2	.	.	.	.
S. lacustris (atypical)	13	6	.	.	.	.	.
Lakes	23	29	13	11	25	17	6

*Sponge weak and with sparse slender spicules—little St. Germaine Lake.

vigorous vegetative growth. It is the only branching form collected by the author which had sufficient rigidity of skeleton to hold its branches upright and maintain its shape when taken from the water (Fig. 4). The one specimen of this species collected from a water low in silica (Little St. Germaine, SiO_2 0.7) was so atypical as to be almost unrecognizable. This specimen was found on the under side of a floating log at the point where the lake narrows down to its outlet. Instead of the rich, strongly lobed to massive, vegetative growth usually associated with this species, it formed a delicate, transparent, whitish film through which the numerous, small, yellow gemmules could be plainly seen. The gemmule spicules, though sparse and scattered, were the short shafted birotulates characteristic of *Ephydatia mülleri.* The skeletal spicules too, although very slender, had the microspining characteristic of the species; so the identification was possible. The fact that the only specimen of this species collected from a water poor in silica was so extremely attenuated, is additional evidence that *Ephydatia mülleri* requires a moderate to high concentration of SiO_2.

Spongilla fragilis, although less restricted than *Ephydatia mülleri,* appears also to be limited by the silica content of the water. The few small specimens collected from lakes low in silica (George, Anna, Bug, and Little St. Germaine) showed weakly developed skeletal spicules, and gemmules almost or completely lacking the usual encrustation of acerates.

Spongilla lacustris, although present in both high and low silica waters, shows marked differences in skeletal development. When collected from a water high in SiO_2, as North Twin Lake, it has long, rigid, almost brittle, lobes which feel rough to the hand and are usually visibly bristling with spicules. In a lake low in SiO_2, as Lake George, the sponge frequently occurs in even greater abundance but the lobes are fleshy and soft. They feel slimy to the touch and collapse to form a shapeless mass when taken from the water. That the ability of the sponge to deposit silica is modified

by some constituent of the water other than silica itself, is suggested by the fact that the size of spicules in a large series of sponges examined was not strictly proportional to the silica content of the water, especially in waters very low in silica. When, however, a series was selected varying both in SiO_2 and other substances in solution as shown by the conductivity, the degree of skeletal development in the lower concentrations merged gradually into the extremely weak condition characteristic of the "atypical" or non-microspined form (Figures 10-16).

Except for differences in degree of skeletal development, *Tubella pennsylvanica* is apparently indifferent to the silica content of the water, since well developed colonies were found in waters of both high and low silica content.

Two species, *Spongilla ingloviformis* and *Ephydatia everetti*, are restricted to the waters of lower silica content. These species are uniformly weak in skeletal development, depending, for shape, upon a tough external membrane or the buoyancy of the water. Spicules are, apparently, not a necessity, but merely an incidental part of their structure since, unlike *Ephydatia mülleri* and *Spongilla fragilis*, specimens with weak spicule development frequently attain large size and numerical abundance. Even in these forms in which spicules might be regarded as unnecessary an increased silica content of the water is, however, accompanied by heavier spicules; thus *Ephydatia everetti* from Bear Lake (SiO_2, 0.8) exhibits much heavier spicules than the same species from Bass Lake (SiO_2, 0.2) or from lakes of still lower silica content. (Figures 2 and 3).

The fact that the "atypical" forms of *Spongilla lacustris* are sharply restricted to waters very low in silica is regarded by the author as a matter of cause and effect rather than of habitat selection. In other words, the low silica content of the water is probably one of the factors which caused those specimens to be atypical, or to fail to develop microspined dermals. That SiO_2 is not the only factor involved in this skeletal modification is indicated by the fact that the typical, or microspined, forms while never collected from the same waters were collected from waters as low in SiO_2 as some of the "atypical" forms.

Silica, then, appears as an important factor in determining the degree of skeletal development, both size and abundance of spicules, in all of the *Spongillidae* studied. Its scarcity, moreover, may be a limiting factor in the distribution of strongly skeletoned forms such as *Ephydatia mülleri* and *Spongilla fragilis*.

RESIDUE AND CONDUCTIVITY OF THE WATER

The total amount of solids in solution in the water, and so left as a residue when the water is evaporated, constitutes the "residue". The residue thus contains both inorganic and organic matter in varying amounts. "Conduc-

tivity", or the readiness with which the water conducts an electric current, depends upon the ionized material present in the water, mostly inorganic salts, and so constitutes an index to the total amount of soluble inorganic matter present. Juday and Birge (1933) have shown that, for the Wisconsin lakes, conductivity is dependent largely upon the salts of calcium and magnesium present, and so correlates closely with bound CO_2, although not identical with it.

TABLE 11. Distribution of sponges with reference to the residue of the water

Sponge	Residue as mgms. per liter							
	11–15	16–20	21–30	31–40	41–50	51–60	61–70	Over 70
E. mülleri	.	.	.	.	5	5	4	5
S. fragilis	.	.	1	2	6	11	10	13
S. lacustris	.	.	6	5	9	12	8	12
T. pennsylvanica	9	7	5	2	7	5	2	5
S. ingloviformis	4	2	.	1	3	1	.	1
E. everetti	12	5	5	.	.	.	.	.
S. lacustris (atypical)	11	7	1	.	.	.	.	.
Lakes	17	20	15	11	12	17	12	16

TABLE 12. Distribution of sponges with reference to conductivity of the water

Sponge	Conductivity as reciprocal megohms							
	7–10	11–15	16–20	21–30	31–50	51–75	76–100	over 100
E. mülleri	.	.		.	4	10	5	.
S. fragilis	.	.	3	1	6	20	10	2
S. lacustris		1	14	4	9	18	9	2
T. pennsylvanica	6	12	11	3	4	6	.	.
S. ingloviformis	4	4	6	.	.	.	.	.
E. everetti	10	12	1	.	.	.	.	.
S. lacustris (atypical)	6	12	1	.	.	.	.	.
Lakes	13	30	21	7	11	28	11	2

A sharp division is shown among the sponges with reference to both of these factors, residue and conductivity, a division, moreover, which shows close correspondence to the way they are associated in nature. For both factors, *Ephydatia mülleri* and *Spongilla fragilis* are restricted to the moderate to higher concentrations, whereas *Ephydatia everetti* is even more sharply restricted to the lower concentrations. Juday and Birge (1933) find that ordinary distilled water has a conductivity of from 3 or 4 to 9, whereas special precautions such as distillation in hard glass are necessary to produce a water with conductivity below 3. Lake waters, then, with conductivity of 7 to 12 are almost as free from minerals as much of the ordinary distilled water. From this we can obtain an idea of the probable sensitivity of a sponge such as *Ephydatia everetti,* which attains its best development in waters having less than 20 mgms. per liter residue and a conductivity below 15. For both

factors, the typical form of *Spongilla lacustris* is tolerant of all but the lowest concentrations whereas the atypical form is restricted to very low concentrations, a highly suggestive fact, although neither residue nor conductivity show a sharp enough distinction between the concentrations tolerated by the two forms to fully explain the fact that they were never found co-existing.

Tubella pennsylvanica appears to be tolerant of the entire range of residue. The absence of this species from 4 lakes having residues above 79 can not be regarded as significant. It is probably limited by the higher conductivities, a fact in harmony with its observed abundance in waters high in organic content and its sensitivity to calcium.

Spongilla ingloviformis alone appears indifferent to residue but sharply limited by conductivity, since it occurs throughout almost the entire range of the former but is limited to very low conductivities. This restriction to waters of low conductivity would account for the fact that this species was never found associated with *Ephydatia mülleri* or *Spongilla fragilis*, whereas the tolerance for waters of high residue would explain the only moderately frequent association with *Ephydatia everetti.*

SUMMARY OF CHEMICAL DATA

To return to the questions raised at the beginning of the discussion, it appears: (1) that the factors favoring *Ephydatia mülleri*, *Spongilla fragilis*, and *S. lacustris*, but inimical to *Ephydatia everetti*, are both high mineral content (Bound CO_2, SiO_2, Conductivity, and Residue in part), and high organic content (accompanying high color and high residue) ; (2) that the factor inimical to *Ephydatia mülleri* and *Spongilla fragilis*, tolerated to a slight degree by *Spongilla lacustris*, but favorable to *Ephydatia everetti* is the extremely low mineralization of the water or absence of solutes, and (3) that the factors favoring *Spongilla ingloviformis* and *Tubella pennsylvanica*, but inimical or indifferent to the remaining forms so far as their presence or absence is concerned, are high color and high organic content. Also that sensitivity to mineral content (indicated by bound CO_2 and conductivity) and to low hydrogen ion concentration (indicated by high pH) may serve to restrict the distribution of these two last named species. The problem of the complete non-association of the microspined and non-microspined forms of *Spongilla lacustris* remains incompletely solved.

Of the physical and chemical factors thus far discussed, four, (Bound CO_2, SiO_2, conductivity, and residue) have shown some degree of correlation with the dissociation of the "typical" and "atypical" forms of *Spongilla lacustris,* however no single factor has shown such perfect correlation as to indicate it as the sole cause of the phenomenon. It appears possible that the explanation may be found in a combination of these four factors. It is well known that among higher animals the ability of an organism to utilize certain food essentials, as calcium, even when provided in abundance, depends upon

the presence also of certain other foods. So it may be that with sponges the ability to form spicules depends not only upon the supply of silicon, but also upon certain other foods associated with the other solutes of the water.

In Table 13 an attempt has been made to secure a single numerical index to all four factors by taking their sum. Because the importance of SiO_2 is obviously disproportionate to the minute quantities found in water, the SiO_2 values have been multiplied by 10. The other values are as given in Table 1.

TABLE 13. Distribution of sponges with reference to the sum of bound CO_2 and residue as mgms. per liter; conductivity as reciprocal megohms, and SiO_2 as mgms. per liter times 10

Sponge	Bound CO_2, Residue, Conductivity and SiO_2 x 10									
	21–25	26–30	31–35	36–40	41–50	51–75	76-100	101–150	151–200	200-up
E. mülleri	.	.	.	.	.	.	.	3	8	6
S. fragilis	.	.	.	.	.	3	.	8	15	17
S. lacustris		.	.	.	4	8	5	8	13	15
T. pennsylvanica	2	6	4	4	3	6	3	7	4	3
S. ingloviformis	.	3	3	1	.	2	3	1	.	.
E. everetti	3	8	5	2	2	.	.	.	.	.
S. lacustris (atypical)	3	6	6	4	.	.	.	.	.	.
Lakes	4	11	9	7	5	9	5	10	17	20

Table 13 shows a sharp separation between the typical and atypical forms of *Spongilla lacustris* found in nature. Furthermore, although *Tubella pennsylvanica* is present throughout practically the entire range, 15 of the 16 lakes from which forms with extremely attenuated spicule development (the "minima" variety) were recorded, are represented in the first four columns of this table; whereas the sixteenth lake, and three of the four lakes listed as containing transitional forms, are included in the fourth and fifth columns (between 37 and 44). It therefore appears that the sum total of solutes in addition to the especially important silicon compounds determine the degree of development of spicules in *Spongilla lacustris* and *Tubella pennsylvanica,* although not their presence or absence.

OPTIMUM HABITATS

Three methods have been frequently used for determining the optimum habitat of animals from purely field data: (1) the absolute frequency of occurrence of the species in question in the various habitats studied; (2) the relative frequency of occurrence, or the frequency of occurrence of the organism over the frequency of occurrence of the environment; and (3) the selection, as an optimum environment, of the conditions under which the species was found most perfectly developed and in greatest abundance.

That the first of these methods may be entirely misleading, is evident if we consider, for example, the distribution of *Tubella pennsylvanica* with

respect to the color of water. This species was collected 18 times in waters with colors below 20, and only 10 times in waters with colors above 100, a fact which would suggest its optimum habitat as uncolored waters. When, however, we note that 59 of the lakes examined had color values below 20, whereas only 13 had color values above 100 (that 30% of the lakes with low color supported this sponge as compared to 77% of those of high color) the fallacy of the method becomes apparent.

The habitat selection of the sponges as judged by their relative frequency may be quickly determined from the tables by comparing the frequency of occurrence of the sponge in any given type of water, with the frequency of occurrence of lakes containing that type of water. In Table 14 the author has used the third method of describing an optimum habitat, the range of conditions in the lakes in which each species was found in greatest luxuriance and profusion. The lakes selected as optimum habitats are as follows (See Table 1):

For *Ephydatia mülleri:* Little Rice, Little Papoose, Tamarack.
For *Spongilla fragilis*: Harvey, Turtle, Little Arborvitae, Little Rice, Dam, Rice.
For *Spongilla lacustris:* Little Pickerel, Rose, Mary, George, Anna.
For *Tubella pennsylvanica:* Helmet, Tadpole, Nellie, Helen, Harvey.
For *Spongilla ingloviformis:* Helmet, Tadpole, Yolanda, Malby, Elizabeth.
For *Ephydatia everetti:* Bass, Larry, Joyce, Louise.
For *Spongilla lacustris* (atypical): Joyce, Larry, Carlin, Katinka, Clear, Walker.

TABLE 14. Range of optimum conditions for Wisconsin *Spongillidae*

Sponge	Environmental conditions						
	Color	Free CO_2	Bound CO_2	pH	SiO_2	Residue	Conductivity
E. mülleri	43–101	1–3	8.4–20	7.0–7.2	2.1–7.0	45–75	45–78
S. fragilis	26–202	0.5–13.9	6.0–21.5	6.6–7.4	2.0–8.2	45–78	33–78
S. lacustris	43–150	1.0–5.5	2.0–8.0	5.4–6.8	0.3–12	33–70	19–28
T. pennsylvanica	97–268	0.5–5.0	0.68–7.0	5.6–6.6	0.4–4.4	39–78	10.8–35
S. ingloviformis	6–268	1.0–5.0	0.88–3.0	5.0–6.0	0.25–4.4	14–71	11–20
E. everetti	6–12	1.2–3.0	0.7–4.5	5.1–6.0	Tr. –0.3	15–18	9–13.5
S. lacustris (atypical)	0–35	0.5–2.0	0.7–4.5	5.1–6.4	Tr. –0.2	15–22	8–17

EFFECTS OF CURRENT AND WATER MOVEMENT

In addition to chemical content, water movement is also of importance in sponge distribution. To *Spongilla fragilis*, and probably also to *Ephydatia mülleri*, it appears to be of considerable importance. The rankest growths of both of these species observed by the author were found in the Wisconsin River and its tributaries, Mud Creek and Rice Creek, in the expanded and

relatively quiet stretch above a power dam west of the village of Eagle River. The construction of the dam had inundated a considerable area of shrubs and trees, many of which had since fallen over and thus provided a large surface for attachment of sponges, as well as an increased organic content due to their decomposition. The water, although without perceptible current, had sufficient movement and interchange with the main channel to prevent stagnation. In this region literally wagon loads of sponges could have been collected. The advantage of gradual water movement over rapid current was evident from a comparison of this stretch of the river with a rapids in the same river a few miles below. The water was essentially the same at both places, no tributaries having entered between. In the rapids the same two species of sponge were still present, encrusting the protected sides of rocks, but the colonies, although numerous, were inconspicuous and small,—rarely over 2 cm. in diameter.

Of the six lakes selected as supporting *Spongilla fragilis* in greatest abundance (Table 14), four had inlets and outlets large enough in proportion to the size of the lake to insure a gradual but constant movement of water through the lake, while in the other two, the profusion of sponges was found where the lake narrowed down to a strait (Turtle Lake) or outlet (Little Arborvitae) so that locally there was continuous water movement. Similar conditions maintain in two of the three lakes where there were optimum growths of *Ephydatia mülleri.*

Spongilla lacustris, although tolerant of current, as evidenced by the fact that it was collected from 14 of the 17 streams examined and was taken from rocks in rapids, nevertheless was found most luxuriantly developed and most abundant in a group of lakes high in organic content but without inlet or outlet, at least during a large part of the season. Old (1932a) collecting from 84 streams and 61 lakes and ponds, found both *Spongilla fragilis* and *Ephydatia mülleri* more common than *Spongilla lacustris*, whereas the author, collecting primarily from lakes found *Spongilla lacustris* by far the most common, a fact which again illustrates the effect of water movement in the distribution of these forms.

Tubella pennsylvanica and *Spongilla igloviformis* are distinctly quiet water species. Of the 46 lakes supporting *Tubella pennsylvanica* and 15 supporting *Spongilla igloviformis*, 36 and 15 respectively are purely seepage lakes. The former sponge, although taken also from streams, was invariably found in quiet protected places where boggy conditions prevailed.

Ephydatia everetti was confined to seepage lakes. This fact can not, however, be interpreted as showing intolerance for current, since only lakes of the seepage type have water of the extremely low chemical content apparently demanded by this species.

Of the sponges less frequently found, *Heteromyenia argyrosperma* was

collected five times each from lakes and streams. Of the collections from lakes, four were made either near the outlet or at the mouth of an inlet where continuous exchange of water would be assured. *Heteromyenia repens* was collected five times from lakes and once from a stream, the water movement varying from the stagnation of a bog (Bug Lake) to a stony riffel. *Heteromyenia ryderi* was taken once each from a slow moving stream and a bog lake, although very poorly developed in the latter. *Carterius tubisperma* was collected twice from riffels and once from a lake at the head of its outlet where continuous water movement was assured. Old also lists this species as preferring streams.

From the observations described it would appear that *Spongilla fragilis*, *Ephydatia mülleri,* and *Heteromyenia argyrosperma,* although tolerant of quiet water, are favored by continuous water movement, that *Spongilla lacustris,* although tolerant of current, is primarily a quiet water species, that *Tubella pennsylvania* and *Spongilla ingloviformis* show a distinct preference for quiet water, whereas *Carterius tubisperma* as distinctly prefers running water.

ECOLOGICAL VARIATIONS OF TAXONOMIC CHARACTERS

GROWTH FORM

Growth forms of sponge colonies have been frequently discussed from the point of view of their use in field recognition of species, or as criteria of sub-species or varieties, though, at the present time, most workers recognize both colony form and texture as too variable to be of taxonomic value.

Old (1932a) summarizes his observations as follows: "Branched colonies are not always *S. lacustris* and colonies of *S. lacustris* are not always branched. Branched colonies are found in *S. aspinosa* and *H. repens*. Short, blunt, finger-like projections are found in *E. mülleri, H. ryderi, H. argyrosperma* and *C. tubisperma.* The writer found unbranched and branched colonies of *S. lacustris* side by side in lakes and streams. The reason for this is not known. . . . Unbranched colonies were held by Annandale (1911) to be the result of unfavorable conditions. This can hardly be true when both forms are found side by side in the same water on similar supports."

From the author's observations it seems that, although certain colony forms may be characteristic of certain species, that no species is limited to any particular form of colony, and that wide variations from the so-called "characteristic forms" are produced by both physical and chemical factors of the environment as well as by age.

Of the species repeatedly collected by the author, one only, *Tubella pennsylvanica,* adhered strictly to a purely encrusting type. Pseudo-branching was common where this sponge had enveloped water roots or twigs; the depth of the colony varied from a delicate, semi transparent film to an incrustation as

much as 10 mm. thick, but no lobed or branched specimens were, at any time, observed.

Spongilla ingloviformis, although usually encrusting, becomes rugose to irregularly lobed (Fig. 8 & 9) under apparently its optimum condition of growth.

Spongilla fragilis, from Wild Cat and Mann lakes, two of the lakes of highest mineral content, formed a firm, almost uniform, incrustation of fine texture and with small, regular, slightly protruding, oscula. In Trout River, Turtle Lake, and Little Arborvitae, the growth was much more robust, the texture looser, the surface less regular, and the oscula larger and more protruding (Fig. 7), whereas, under conditions of its most luxuriant growth found above the Wisconsin River dam, the surface developed irregular lobes and protrusions suggestive of incipient branching (Fig. 5 & 6). Although fineness of skeletal texture and regularity of pores have both been used as criteria of varieties or sub species in *S. fragilis*, the author is inclined to regard them as influenced both by current and by the relative abundance of skeleton-building materials and organic foods, an irregular surface resulting from a rapid growth produced by high organic content, in the absence of a proportionately high mineral content for skeleton building.

Spongilla lacustris exhibits every variation in form from simple encrustations to tufts of long, slender, finger-like processes. Although no single factor is responsible for the entire range of forms, the age of the colony, area and slope of the surface to which it is attached, wave action, and chemical content of the water, are all regarded as influencing the growth-form of this species. Repeated observation of the same colony during the summer of 1932 showed that colonies which were encrusting in early July had become abundantly branched by the third week of August, whereas younger colonies on the same log, not observed at all at the time of the first visit, were still encrusting; a fact which may explain the observation of Old (1932a), that branching and encrusting colonies may be found side by side in the same habitat. Encrusting sponges are more frequently found on broad surfaces, such as planks or large logs, than on slender attachments, such as twigs. They are also commoner on the under side of the support than on the upper side. This latter condition was well illustrated by observation of the sponges in a pile of old timber in Little Rice Lake. Numerous large colonies of *S. lacustris* were found encrusting the under sides of these timbers, but only beginning to branch along the edges where the colony was growing in a vertical direction. Colonies on the upper sides of similar timbers began their branching in the central, or older, portion rather than at the edges. That this inhibition to branching was the result of gravity or the inverted position, rather than of shade, is evidenced by the fact that colorless but branching colonies have been collected from under bridges and other shaded locations.

Water movement, unless strong, has no apparent effect upon the branching of *Spongilla lacustris.* Except right in riffels, where only encrusting forms are found, the sponges of streams show the same type of branching as those of the lakes drained by the streams. Strong wave action may inhibit the development of branches. An excellent illustration of the varieties of growth form produced by physical factors was observed in Lake Anna. Here a large tree trunk almost covered by *S. lacustris,* sloped gradually from above the surface to a depth of about 2.5 meters. The situation, in the lee of an island, although not completely protected from wind, was sheltered from strong wave action. The sponges were encrusting on the under side of this log; they became irregular and lobed as they rounded the sides, and strongly branched on the upper surface. Another gradient was observed along the upper side of the log, from the water's edge to below wave action. Near the surface of the water the branches were short, thick, and irregular knob shaped; at two decimeters depth they were 4 to 5 centimeters long and somewhat club shaped, whereas at a depth of 0.5 to 1.5 meters they were of the typical finger shape, and 10 to 12 centimeters long. Vaughan (1919) describes a similar relationship between growth forms of corals and depths of water and violence of wave action. Specimens from waters high in organic matter tend to have numerous long, fleshy, closely crowded and frequently anastomosing branches, whereas specimens from waters low in organic matter but high in mineral content are more sparsely branched and the branches are independent, more slender, and of more uniform diameter. The extreme of this latter type was collected from North Twin Lake, a small, shallow, bog lake with a barren peat bottom, but very high in silica. In this lake the *Spongilla lacustris* bore branches 3 to 4 decimeters long but only 7 or 8 mm. in diameter, and not more than 2 to 3 branches to one small basal part. The long branches, in part reclining on the bottom and in part ascending, might better be described as worm-shaped than as finger-shaped. Their texture was poor in fiber but so rich in spicules as to render them brittle and "scratchy" to the touch.

Ephydatia everetti (Mills) 1884 is described by Potts as "without sessile portion, but consisting altogether of slender meandering filaments little more than a sixteenth of an inch in diameter." Although this describes the growth form of *E. everetti,* when collected from its usual attachment (aquatic vegetation such as Eriocaulon or Isoetes) or from an irregular surface, still specimens having an extensive sessile portion, and even encrusting colonies, have occasionally been taken in the same locations, from larger more uniform attachments such as fallen trees.

While, in general, it appears that after a sponge has once encrusted its base of support, a rapid growth tends to produce an irregular, undulating, rugose, lobed, or branching surface, still there are so many factors affecting

growth form that any statement to the effect that encrusting colonies indicate unfavorable conditions, are an adaptation to current, are an abnormality, or even are younger, seems wholly unwarranted.

SPICULE DEVELOPMENT

FIELD OBSERVATIONS

Since the classification of the *Spongillidae* is based largely upon skeletal parts, especially the spicules surrounding the gemmules, any variation in spicules produced by the environment is certain to be of taxonomic, as well as of ecological interest.

Under the discussion of SiO_2 it was pointed out that, in waters of low SiO_2 content, the size and number of spicules is greatly reduced; that in *Ephydatia mülleri* and *Spongilla fragilis* the spicules associated with the gemmules tend to disappear, and the entire skeletal structure to become delicate and attenuated, in waters of mineral content near the lower limit of tolerance of the species; and that similar variations have been observed in other species.

Figures 2 and 3 show gemmule, dermal, and skeletal spicules of *Ephydatia everetti* from waters having 0.2 and 0.8 mgms. per liter SiO_2 respectively. The vegetative parts of these two sponges were equally thrifty and well developed. If spicule measurements can be accepted as a criterion of varieties, one can find here a variety difference, however a complete series connecting these two can be established by considering materials from the entire 22 lakes from which this species was collected.

Figures 10 to 16 are microphotographs of the spicules of *Spongilla lacustris* collected from seven different lakes (North Twin, Papoose, Rock, Nebish, Mary (near Papoose), Katinka, and Joyce) arranged in order of descending silica content. The magnication is the same throughout the series. From North Twin to Nebish a progressive attenuation of spicules, both skeletal and dermal, is apparent. The skeletal spicules in the latter, although longer, are no greater in diameter than the dermal spicules in the former. The dermal spicules, while still present, and still microspined, in the specimen from Nebish, require careful adjustment of the microscope and light to ascertain the fact.

From this observation as to the correlation of spicule reduction and decrease in skeleton forming material in the water, one would expect that a still further decrease in SiO_2 might reduce the skeletal spicules and, eventually, eliminate the dermals altogether. In this event, one should expect the skeleton-poor *Spongilla lacustris* to look just like the "atypical" specimens of *S. lacustris* shown in the next two figures (Figures 14 and 15). The spicules from Mary Lake (Fig. 14) show a condition frequently found in these sponges from soft-water lakes, an abundance of spicules variable in

size and intermediate in character between skeletal and dermal spicules. Similar spicules were described by Potts, 1887, for *Spongilla aspinosa.* In Fig. 15, the spicules from Lake Katinka, the group of small transparent spicules at the upper left of the picture are apparently of organic material, either lacking silica or so poor in that substance that they do not refract light as do ordinary spicules. The spicules from Joyce Lake (Fig. 16) show about the last stage in spicule reduction, as here, not only the dermals, but frequently even the skeletal spicules, are poorly or incompletely silicified and reduced to the verge of total disappearance.

While these seven types apparently form an intergrading series, and while the series would be still more complete and minutely intergraded if all of the specimens collected were considered, still, in as much as the presence of microspined dermal spicules is a species characteristic of *Spongilla lacustris,* the absence of these dermals places the sponges shown in the last three figures into a separate species, either *Spongilla aspinosa* Potts or a new species. At least, had the author's collections been less extensive, she would not have questioned the presence of two distinct species. It is possible, of course, that the difference between the sponges possessing and those lacking microspined dermals may be genetic, thus indicating two different species; yet, the field data all indicate a single species variously modified by environment. This latter interpretation is indicated by (1) the intergradation of the two forms as has been described, (2) the fact that the two forms, although both abundant in the limited area studied, have never been found coexisting in the same body of water, (3) the apparent correlation between degree of spicule development and the mineral content, especially SiO_2, of the water, and (4) the fact that a fluctuation in the water of one lake was accompanied by a change in the type of sponge found in it. Trilby Lake (Table 1), in 1932, showed no detectible amount of SiO_2. At this time the extreme soft-water or "atypical" form of sponge was collected in abundance. Two years later, a very dry year, the SiO_2 had increased to 0.5 mgms. per liter accompanied by a doubling in the amount of carbonates. At this time, not a specimen of the sponge lacking microspined dermals could be found; the sponges, although as abundant as formerly, were all the "typical" *Spongilla lacustris,* similar in spicule development to those from Nebish Lake (Fig. 13).

The extreme variations in *Tubella pennsylvanica* have already been mentioned. Between the extremely attenuated forms described earlier in this paper and the "typical" forms, were a great variety of modifications (Figures 17-22) including irregular, incised, and star shaped, rotules (both distal and proximal), and proximal rotules with rays or "spokes" of greater thickness from the shaft to the margin, and with lobed margins. Potts (1887) describes a somewhat similar series of variations found by him in *T. penn-*

sylvanica. Beginning with Bear Lake, an upper source of the Lehigh River at an altitude of 1800 ft., he found an extremely delicate form designated by him as *Tubella pennsylvanica var. minima.* Collections made from the same river at altitudes of 1200, 1000, 600, and 40 to 50 ft. showed progressively heavier spicules and closer approximation in size of the two rotules. According to Potts, "These changes followed closely the lines of increasing altitude; their *cause* must be left for later determination."

If, now, the Tubellas collected in Wisconsin, are arranged not in order of altitude, which varies but little in this region, but in order of increasing mineralization of the water, one can construct a series similar to that of Potts. Beginning with such lakes as Little Rudolph or Little John, Jr., in which the characteristics of Potts' "minima" are equalled or surpassed, and ending with the outlet of Mann Lake, where the heavily spiculed sponges may be regarded as "typical," we have all except the extremely heavily spiculed forms found, by Potts, near the coast. The explanation is doubtless the same in the two series, an increase in SiO_2 and mineral content of the water. Mountain lakes, which form the very head-waters of rivers (such as Bear Lake studied by Potts) are usually bodies of pure, soft water. As the stream winds its way to the coast, augmented by drainage and ground waters, it becomes progressively more highly mineralized, and such variations in the mineral content of the water would be reflected in the skeletal development of the sponges growing in it.

EXPERIMENTAL STUDY

Although field data indicate, in case of both *Spongilla lacustris* and *Tubella pennsylvanica,* that the wide range of spicule forms observed was the product of variety in environments, still, before any definite conclusion could be drawn it remained to test experimentally whether environment alone could produce such extreme variations as were found in nature. To make this test colonies of both species were transferred from Little Rudolph Lake; (conductivity 5.6 to 8.2 and SiO_2 merely a trace) a water from Trout Lake, (conductivity 75 and SiO_2 7.3) and the spicule modifications observed by examination of fragments of the colonies from time to time. For the purpose of the transfer a clean wooden barrel of 15 gallons capacity was used. In preliminary experiments, in which galvanized iron tubs were used, the sponges invariably died. The barrel was soaked a week in Trout Lake, then sunk three fourths of its depth in the sand to guard against rapid changes in temperature, and filled to about a third of its depth with sand. Fresh water from Trout Lake was pumped into the barrel mornings and evenings, and, during very hot weather, at three hour intervals during the day. As the only sponges found in Trout Lake had been collected from a bay at the head of its outlet almost two miles distant from the Biological Survey

headquarters, the chance of introducing sponge fragments or gemmules with the water was regarded as negligible. In order to provide a water of higher organic content than that of Trout Lake, about two gallons of bog water was added each time the water in the barrel was renewed. The Forestry Bog, from which this water was secured, had a conductivity of 9.5 to 12.0, SiO_2 1.4, and color of 70, and was without sponge fauna. A typical analysis of water from the barrel showed free CO_2 4.75, bound CO_2 9.5, pH 6.9, SiO_2 3.0, conductivity 40, and color 38.

In transferring the sponge colonies from Little Rudolph Lake care was taken that they should never be lifted from the water. As controls a piece of each colony transferred was removed for examination at the beginning of the experiment, and marked colonies left in Little Rudolph Lake were collected for examination at the close of the experiment.

DATA

The experiment was begun July 18 and terminated August 20, 1934. Fragments of the transferred colonies were examined July 28 and August 11 as well as at the beginning and close of the experiment. No change in spicule form occurred in the colonies left in Little Rudolph Lake as controls during the 33 days of the experiment. In each of the colonies transferred, however, the type of spicules changed completely, from the attenuated forms characteristic of extremely soft waters to the more robust forms usually found in waters of moderate mineralization. (Figures 20-25).

Detailed examination of several of the colonies made at the close of the experiment showed that the older parts of the colony, the parts matured before transfer from Little Rudolph Lake, still had the extremely slender type of spicules; the new parts of each colony, the advancing edges and newly formed lobes, had only the robust spicules formed in the water of higher silica content, whereas the zone of transition between old and new structure, the areas which were at the very edge of the colony at the time the transfer was made, showed a mixture of the two types of spicules. This would indicate that spicules, when once formed, can not make a second growth ever under conditions of abundant building material.

The extent to which the character of the spicules was altered by a change in the mineral content of the water is best seen by a study of Figures 18 to 25. The magnification is the same for all figures on this page. Figure 18 is a group of gemmule birotulates and the tip of one skeletal spicule of *Tubella pennsylvanica* from Little Rice Lake, a lake comparable to Trout Lake in silica content of water, but higher in organic content, hence more favorable for this species. The figure shows both the shape and overlapping arrangement of gemmule birotulates usually found in this species. Figure 19, a gemmule birotulate from a specimen collected from Percy Lake, shows the reduced distal rotule, long slender shaft, and lobed proximal rotule fre-

quently observed in material collected from soft water lakes. Figures 20 and 21 show gemmule birotulates from control material collected from Little Rudolph Lake. These are characterized by incised to stellate proximal rotules, knob shaped to stellate distal rotules, long slender shaft, and sparse distribution in the gemmule wall (Fig. 21). Figure 22 is a group of skeletal spicules from the same colony. In contrast to Figures 20-22, Figure 23 shows a group of spicules from the same colony after 33 days under the conditions of the experiment. The material on this slide was taken from the region of transition, or the part of the colony which was still developing at the time the sponge was transferred to a more highly mineralized water. The gemmule birotulates shown are all from the new growth and are comparable to those shown in Figure 18. The contrast between skeletal spicules developed in Little Rudolph Lake and those developed after transference to a water of higher silica content is brought out by comparing the acerate spicules in the center of the figure with those at the extreme right and left.

Similar modifications of the spicules of *Spongilla lacustris* are illustrated in Figures 24 and 25. Figure 24 shows three of the skeletal spicules and a group of the minute nonspined dermal spicules from a control specimen from Little Rudolph Lake. Figure 25, a microphotograph from the transitional part of the same colony after development in the experimental water, shows one microspined dermal spicule (in the upper part of the figure) and part of one skeletal spicule (diagonaling the figure from upper left to lower right) belonging to the new growth, as compared to a group of spicules (lower part of the picture) developed before the transfer was made. It will be observed that the dermal spicule developed under the conditions of the experiment is of greater diameter than the skeletal spicules developed in Little Rudolph Lake. Although the magnification is greater, a comparison of the spicules formed after the transfer with the spicules of sponges collected in nature from water of moderate hardness (Figs. 10-12) shows that they are in every way comparable.

It can be concluded, then, on the basis of both field observation and experiment, that the great variety of spicule sizes and forms exhibited by both *Tubella pennsylvanica* and *Spongilla lacustris*, represent somatic modifications produced by the environment, not incipient species. Furthermore, in as much as this great variety of spicule-form is apparently produced by a variety of natural conditions under all of which the sponge is able to grow and reproduce normally, it follows that no one type of spicule can be selected as "typical" or "normal" and the others regarded as "abnormal". Moderately hard waters are more common than waters of conductivity below 20; the types of structures they produce are, therefore, more common; this does not, however, make them any more normal. They are all normal responses of a normal organism in one of its normal natural environments; and any adequate taxo-

nomic definition made for such a variable species must be sufficiently flexible to include its normal natural variations.

A Question of Nomenclature

Although the purpose of this study has been purely ecological, the necessity of using names with which to designate the sponges collected has forced the author to make one decision for herself in the field which belongs primarily to taxonomy. As in using the name "*Tubella pennsylvanica* Potts, 1882", the author is at variance with at least two contemporary workers on the *Spongillidae,* who designate the same species as "*Trochospongilla pennsylvanica* (Potts) 1882", some explanation of this adherence to the older name seems in order.

The Genus Tubella, established by Carter in 1881, was based upon four South American species, all characterized by gemmules having a granular crust charged with trumpet-shaped, inaequibirotulate spicules, the larger rotule of which rests upon the chitinous coat; the size of the outer rotule smaller, but having a variable relation to that of the former. In all four of the species placed in this genus by Carter, the larger rotule is described as having an even circular margin; although in two, the smaller rotule is described as toothed.

The following year, a fifth species, *Tubella pennsylvanica,* was described from North America by Potts. During the five succeeding years the same author received specimens of this species from many parts of this continent, including Newfoundland, and, by comparison of a large series of specimens, was able to describe many variations found within the species. These variations included not only extreme differences in robustness of spicules and relative diameter of the proximal and distal rotules, but even a toothed or rayed condition of the smaller rotule, and, in one form, a division of the larger rotule into uneven rays or rounded segments. Thus the extreme variability of *Tubella pennsylvanica* was clearly stated by Potts as early as 1887.

The Genus Trochospongilla was established by Vejdovsky in 1883, for two species having "amphidiscs smooth with entire margins", and, again, he described the gemmules as "covered with spool-like amphidiscs whose rotules have entire margins".

Potts (1887 and also 1918) accepts Vejdovsky's genus, and makes it clear that Trochospongilla is distinguished by entire margined *equal* rotules, whereas Tubella has more or less *unequal* rotules, which are usually, but not uniformly, entire, and that the shaft connecting the rotules is, in Tubella, more or less swollen at the end adjoining the proximal (larger) rotule.

Annandale (1911) redefines the genera Tubella and Trochospongilla, and places Potts' species in the latter genus, making it *Trochospongilla pennsylvanica.* According to his definition, the genus Trochospongilla is charac-

terized by its smooth margined birotulates, irrespective of variations in diameter, whereas "Tubella" is reserved to designate forms in which the unequal birotulate discs differ not only in size but also in form; the smaller disc is a rounded knob, the larger serrated and flat. In making this redefinition, Annandale completely ignores the numerous variations in form of rotule existing in the species under question.

Gee (1932 and 1933) accepts the revision of Annandale with the added qualification that the trumpet-like birotules of Tubella have comparatively longer shafts than those of Trochospongilla. In discussing his materials of *T. pennsylvanica*, Gee says, "While the rotules are generally circular, yet asymmetrical ones frequently occur and I have found some of the small rotules to be distinctly incised; also the lower rotules in some specimens recently examined have decidedly irregular edges which frequently are provided with rounded incisions or lobes rather than angular indentations. This state of affairs raises the question as to whether this form may not really be a connecting link between the *Tubellas* and the *Trochospongillas*." Again, after figuring distinctly toothed distal rotules, he says, "This last mentioned characteristic brings this form very close to the genus *Tubella* and leads us to wonder if it may not be a more or less transitional form connecting up the two genera *Trochospongilla* and *Tubella*. It is possible to find connecting links between the extremes and we know therefore that they represent the same sponge."

After examining 192 different specimens from 46 lakes and 3 streams of northeastern Wisconsin, the author finds, in that limited area, practically all of the various modifications and variations described by Potts and by Gee, as well as specimens in which the birotulates vary greatly in relative length of shaft as compared to diameter of rotules, and specimens in which the larger rotule is distinctly incised. Having found all intergradations, the author, like Gee, is convinced that a single species is represented. In addition, the author finds a distinct correlation between certain of these variations in structure of spicules and the chemical content of the water from which the sponge was collected. Instead, then, of being interpreted as incipient species connecting the genera Trochospongilla and Tubella (as Gee would apparently interpret them) these variations are regarded as ecological varieties; somatic modifications produced by the environment. If this interpretation is accepted and Annandale's separation of the genera Tubella and Trochospongilla on the basis of the margins of the rotules is recognized, one is confronted by the absurdity of supposing that the kind of water a sponge grows in can change its genus without changing its species. To avoid this dilemma, the author reverts to the generic definitions accepted by Potts. The genus Tubella is then distinguished by inequality of rotules and greater diameter of the shaft near the proximal rotule, whereas the genus Trochospongilla has equal rotules

with the ends of the shaft similar. If these generic criteria also prove "shifting sand", then by the law of priority, it is the genus Trochospongilla which must pass into synonymy; but, in either event, the species under question remains as originally named, *Tubella pennsylvanica* Potts 1882.

There is one further reason for adhering to the definitions of the genera Tubella and Trochospongilla as accepted by Potts and for considering that the species pennsylvanica should be retained in the genus Tubella. *Tubella paulula* (Bowerbank) 1863, Synonym *Spongilla paulula* Bowerbank 1863, is the type species of the genus Tubella, yet, in revising the genera according to Annandale's redefinition, Gee (1932) lists this species in the genus Trochospongilla. Now if the author correctly interprets the rules of nomenclature, the type species of a genus is the one fixed point of the genus and, so long as the genus stands, can not under any circumstances be transferred to a subsequently established genus. *Tubella paulula* must, therefore, remain in the genus Tubella. While the author has not had the opportunity of examining original materials, yet a comparison of her specimens of *Tubella pennsylvanica* with the descriptions and excellent figures of spicules of the various species of Tubella and Trochospongilla given by Gee (1931 and 1932) convinces her that the species pennsylvanica most closely resembles *Tubella paulula* in form of gemmule birotulates, and was, therefore, rightly placed in the same genus by Potts.

Spongilla Aspinosa

Since the presence or absence of microspines on the dermal spicules is the criterion which separates *Spongilla aspinosa* Potts 1880 from *Spongilla lacustris,* and since microspines may be lacking from the dermal spicules of *S. lacustris* grown in water lacking silica, the question naturally arises, Is *Spongilla aspinosa* a valid species or did Potts describe, as a distinct species, these silica poor forms of *S. lacustris?* To answer this question the author examined specimens of *S. aspinosa* collected by Potts from the type locality, Absecum, New Jersey, and kindly loaned for the study by the Academy of Natural Sciences of Philadelphia, and the United States National Museum. A microphotograph of this rare species, showing the end of one skeletal spicule and several dermal spicules, is given in Figure 26. A comparison of this figure with the silica poor *S. lacustris* (Fig. 24) shows at a glance that the robust, well defined, glassy looking dermal spicules of *S. aspinosa,* are distinct from the barely visible, incompletely silicified spicules of the silica deficient *S. lacustris.* So far as the author's work is concerned, *Spongilla aspinosa* Potts stands as a valid species.

SUMMARY

1. As the result of an examination of 127 lakes and 17 streams in northeastern Wisconsin 10 species of *Spongillidae* were discovered, of which one,

Ephydatia everetti, has not previously been reported for the state or the Great Lakes region. Six species were found in sufficient abundance to permit an ecological study of their habitats.

2. *Ephydatia mülleri* is usually found associated with *Spongilla fragilis* and *S. lacustris,* although differing from these two species in that it is less tolerant of waters extremely low in mineralization. It was never taken in waters having a bound CO_2 content below 5 mgms. per liter or a conductivity below 30 reciprocal megohms.

3. *Ephydatia everetti* and *Spongilla ingloviformis,* on the other hand, are restricted to waters low in mineral content, neither species having been found in waters having a bound CO_2 above 5 mgms. per liter or conductivity above 20 reciprocal megohms. The two species differ in that *E. everetti* is restricted also to waters low in SiO_2, color, and organic content, whereas *S. ingloviformis* appears indifferent to SiO_2 content and is favored by high color and high organic content.

4. *Spongilla lacustris,* although occurring throughout the entire range of conditions found, attains its best development in small lakes of high color and organic content and rather low mineralization.

5. The habitat selection of *Spongilla fragilis* is similar to that of *Ephydatia mülleri* except that it has a wider tolerance for practically all of the factors studied.

6. *Tubella pennsylvanica* was found widely distributed throughout the range of conditions studied, except that it was absent from the more basic and more highly mineralized waters. Like *Spongilla ingloviformis,* with which it is frequently collected, it is distinctly favored by bog conditions, high acidity, color and organic content.

7. Transparency of water is important in determining the position of sponges with respect to depth and shade, but not their presence or absence from lakes. *Ephydatia everetti* was collected at a depth of 3.5 meters in transparent water. No species, not even among those ordinarily restricted to shaded situations, was taken at a depth below the penetration of visible light rays.

8. Continuous water movement, not strong current, seems to favor *Ephydatia mülleri* and *Spongilla fragilis,* and to be necessary for a good growth of *Heteromyenia argyrosperma* or *Carterius tubisperma. Spongilla lacustris* shows better development in standing waters provided they are high in organic content, whereas *Tubella pennsylvanica* and *Spongilla ingloviformis* are practically restricted to such conditions.

9. Growth form of colonies is believed to be affected by age, current or wave action, area, smoothness and slope of the base of support, and amounts of organic and mineral solutes in the water.

10. Skeletal development is greatly influenced by the mineral content of

the water, especially SiO_2. In waters of SiO_2 content below 0.4 mgms. per liter and of low conductivity and total solutes, *Spongilla lacustris* shows a progressive attenuation of its spicules, eventually losing its microspined dermal spicules (an important species character). These skeleton-poor forms appear no less vigorous and thrifty than heavily-spiculed specimens from more highly mineralized waters. Similarly *Tubella pennsylvanica* shows marked variations correlated with the degree of mineralization of the water. These entirely normal variations, in some cases, abrogate accepted generic criteria.

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EXPLANATION OF PLATES

PLATE II—FIGS. 2-9

FIG. 2. *Ephydatia everetti* from Bass Lake, SiO_2, 0.2 mgms. per liter, showing skeletal spicules (acerates), gemmule spicules (large birotulates) and dermal spicule (small birotulate).

FIG. 3. *Ephydatia everetti* from Bear Lake, SiO_2, 0.8 mgms. per liter. Magnification the same as Fig. 1.

FIG. 4. *Ephydatia mülleri* from Little Rice Lake, showing a characteristic growth form.

FIG. 5. *Spongilla fragilis* from the Wisconsin River above a power dam. Observe irregular surface and protruding oscula.

FIGS. 6 and 7. *Spongilla fragilis,* dried specimens showing differences in skeletal structures. From the Wisconsin River and outlet of Trout Lake respectively.

FIGS. 8 and 9. *Spongilla ingloviformis,* from Helmit Lake, showing large size and rugose surface developed under optimum conditions, also heavy external membrane and inconspicuous pores (Compare with *Spongilla fragilis,* Fig. 5).

PLATE II—FIGS. 10-17

FIGS. 10-16. Spicules of *Spongilla lacustris* from lakes of differing SiO_2, contents. Magnification the same in all figures.

FIG. 10 from North Twin Lake, SiO_2 content 1.3 mgms. per liter.

FIG. 11 from Papoose Lake, SiO_2 content 1.6 mgms. per liter.

FIG. 12 from Rock Lake, SiO_3 content 0.6 mgms. per liter.

FIG. 13 from Nebish Lake, SiO_2 content 0.4 mgms. per liter.

FIG. 14 *(lower left of plate)* from Mary Lake, SiO_2 content 0.25 mgms. per liter.

FIG. 15 *(center right of plate)* from Katinka Lake, SiO_2 content trace.

FIG. 16 from Joyce Lake, SiO_2 content trace.

FIG. 17. *Tubella pennsylvanica,* fragment of a gemmule, from a moderately soft water, Nellie Lake, showing inaequibirotulates with slender shafts, irregularly rayed proximal rotules, and knob shaped distal rotules.

PLATE III—FIGS. 18-26

FIGS. 18-23. Spicules of *Tubella pennsylvanica.* Magnification the same in all figures.

FIG. 18 from Little Rice Lake, SiO_2 content 7.0 mgms. per liter.

FIG. 19 from Perch Lake, SiO_2 content trace.

FIG. 20 from Little Rudolph Lake, SiO_2 content trace.

FIG. 21 part of a gemmule from Little Rudolph Lake, showing shape and sparse distribution of birotulate spicules characteristic of this species from very soft waters.

FIG. 22. Skeletal spicules of the same specimen.

FIG. 23. Gemmule and skeletal spicules from the same colony as figures 21 and 22, after 33 days of development in water of silica content 3.0 mgms. per liter. All gemmule spicules shown developed after the transfer. Skeletal spicules developed before and after transference to water of higher SiO_2 content are easily distinguished.

FIG. 24 and 25. *Spongilla lacustris* from Little Rudolph Lake.

FIG. 24. Three skeletal spicules and a group of dermal spicules from a colony collected from Little Rudolph Lake.

FIG. 25. Spicules from the same colony after 33 days of development in water of SiO_2 content 3.0 mgms. per liter. The two spicules crossing near the top of the picture developed in the water of higher SiO_2 content. The spicules near the bottom of the picture matured while still in Little Rudolph Lake.

FIG. 26. *Spongilla aspinosa* Potts. End of one skeletal spicule and several dermal spicules. This species is not to be confused with the forms of *Spongilla lacustris* which have non microspined dermal spuicules due to lack of silica in the water (Fig. 24).

PLATE I

PLATE II

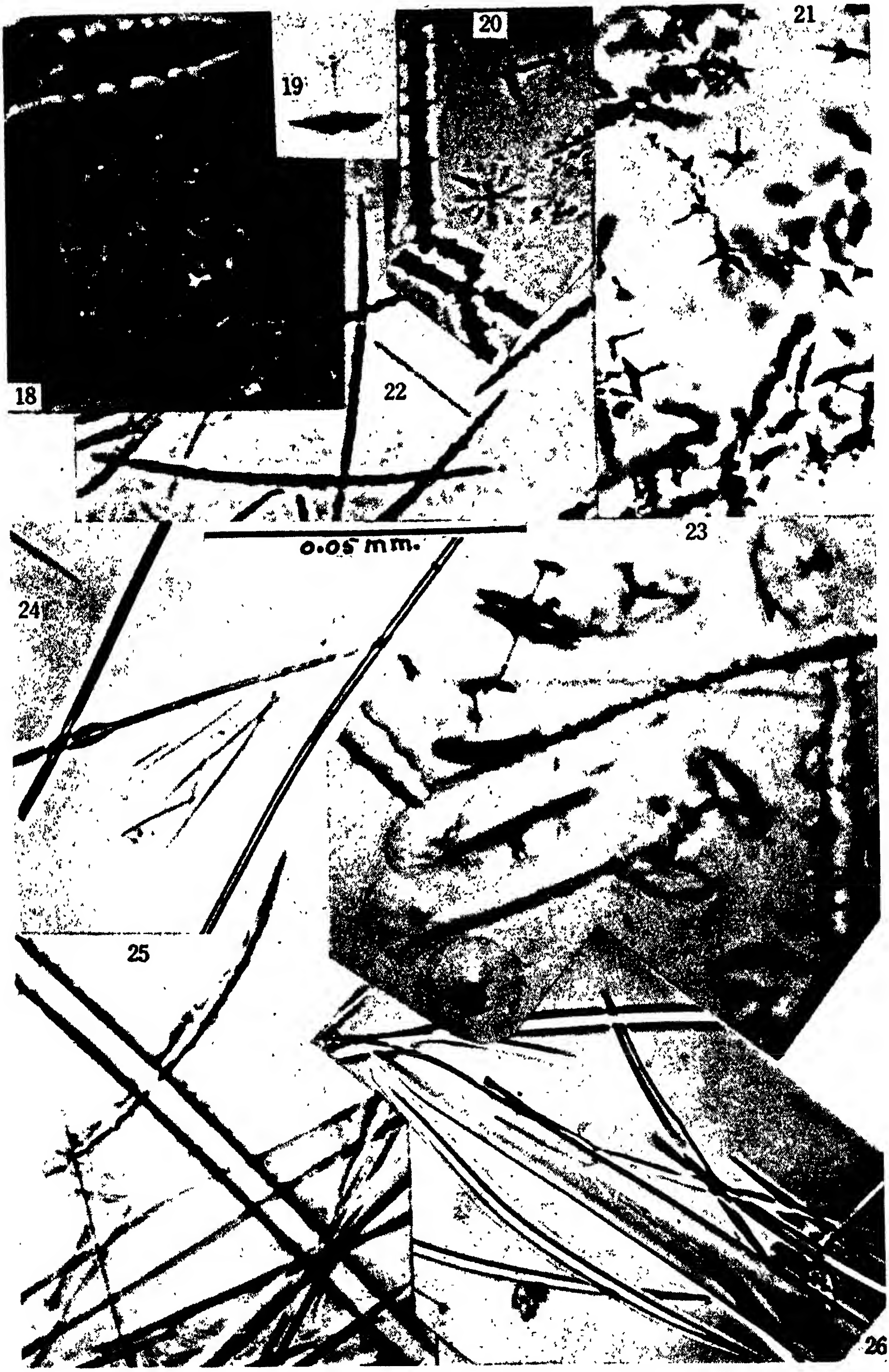

PLATE III

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